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Problems in catfish anatomy and phylogeny exemplified by the Neotropical Hypophthalmidae (Teleostei: Siluroidei)

Gordon J. Howes

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Introduction

Of the subgroups of otophysan fishes, the siluroids—or catfishes—are the most morphologically diverse. None of the other subgroups, gymnotoids, characoids and cyprinoids, has such a range of body shape, peculiarity of dermal covering when present, and cranial morphology. Neither do these groups display such a range of postcranial architecture, complex fusion patterns of the caudal fin skeleton or such diverse forms of swimbladder. This morphological diversity is reflected in the most recent familial classification of the siluroids (Greenwood *et al.*, 1966), which recognises thirty-one families, a number exceeding the combined familial total of other otophysan groups.

As presently recognised, most siluroid families are morphologically well differentiated, suggesting that each is probably a monophyletic assemblage. Indeed, the large morphological 'gaps' separating families are emphasised by the fact that seven families are monotypic, cf one among characoids and two among gymnotoids. That the interrelationships of siluroid families have scarcely been studied is not surprising when one considers the paucity of anatomical data available. Even the largest families, i.e. the Pimelodidae, Ariidae and Bagridae are represented in the anatomical literature by only meagre information, the anatomy of some neotropical families, Auchenipteridae, Ageneiosidae, and Aspredinidae, has scarcely been described.

The siluroids offer a wealth of character complexes involving the bony elements of the cranium, vertebral column and fin supports, and their associated muscles. These character

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complexes lend themselves readily to the application of cladistic methodology. The task of analysis is, however, a daunting one. Not only is the number of taxa considerable, over 2000 species, but, by their very nature, siluroids are difficult to study. Most adult specimens are large and highly ossified, and sutures between bones are often obscured in dry skeletal material. It is therefore necessary to work, for the most part, with cleared and stained preparations of small, and frequently juvenile specimens. Thus problems can arise in the interpretation of features which undergo considerable ontogenetic change.

One of the generalisations made about siluroids is that they are benthic fishes. In fact, the majority of species in seven families, Siluridae, Schilbeidae, Pangasiidae, Ariidae, Ageneiosidae, Cetopsidae, Hypophthalmidae, are mid-water to surface dwellers, and only in one third of families, Loricariidae, Amphiliidae, Callichthyidae, Astroblepidae, Doradidae, Chacidae, Sisoridae, Cranoglanididae, can the majority of included taxa be classed as entirely benthic. In the past more attention has been given to siluroid inter- than to intra-relationships. The most recent analysis (Fink & Fink, 1981) recognises the siluroids as a suborder, the Siluroidei, coordinate with their supposed sister group, the Gymnotoidei which together form the order Siluriformes. The Siluriformes are, in turn, thought to be the sister group of the characoids, order Characiformes, with the cyprinoids, order Cypriniformes, representing the plesiomorph lineage and sister group of the Silurifomes + the Characiformes.

Only the most rudimentary analyses have been attempted on the functional anatomy of siluroids (Eaton, 1948; Alexander, 1965; Gosline, 1973 & 1975). According to Gosline (1973) siluroids employ a feeding mechanism functionally different from that of other otophysans. But again, lack of comparative anatomical data prohibits any worthwhile discussion of this issue.

One attempt at cladistic analysis involving several siluroid families has been published by Lundberg & Baskin (1969). In order to obtain an understanding of siluroid relationships these authors chose to focus efforts '. . . on comparative studies of a single structural complex in obtaining an understanding of siluroid relationships'. This approach, whilst accumulating valuable comparative data, can however, produce a misleading phylogeny. The weakness inherent in an approach that places reliance on single character complexes is discussed below (p. 27) with reference to patterns of vertebral fusion and swimbladder encapsulation.

Roberts (1973) notes that the '. . . cosmopolitan distribution of siluroids and their pseudarchaic characters have led ichthyologists to believe catfishes to be older than other ostariophysans'. I presume 'pseudarchaic' as used by Roberts means 'neomorph' resulting in convergences with features found in ancient groups. But, neomorphs are no indication of the group's phyletic age. On the other hand, the cosmopolitan distribution of siluroids may suggest an early and extensive distribution whereas the more restricted distribution of other otophysans could indicate their later cladogenesis from the ancestral otophysan lineage.

The subject of this paper, the family Hypophthalmidae, is chosen for anatomical investigation because it represents several aspects of the problems discussed above. The family is monotypic, apparently 'isolated' phyletically, is 'pelagic' in habits, and poses intriguing problems of functional anatomy. The object of the study is to describe the osteological and myological features, with particular regard to the cranium, to analyse these features in terms of their apo-plesiomorphic status, to account for their functional relevance, and to use these data as indicators of phyletic relationship.

Günther (1864:3:66) first recognised the distinctiveness of *Hypophthalmus* by placing it in a separate subfamily, Siluroidae Anomalopterae (Group Hypophthalmina). *Helogenes* was also included on the basis of its elongate anal fin, and its short dorsal and adipose fins. Cope (1871) established the Hypophthalmidae as one of three families of his Nematognathi. In Cope's view *Hypophthalmus* was so aberrant that he doubted its relationships with other catfishes. Eigenmann & Eigenmann (1890) continued to recognise Günther's concept of the family but Regan (1911) placed *Helogenes* in a separate family thereby establishing the Hypophthalmidae as monotypic. Chardon (1968) chose to recognise the uniqueness of the

Hypophthalmidae by placing it in its own suborder, the Hypophthalmoidei. He was, however, unable to relate the taxon closely with another of equal rank.

As yet, the taxonomy of the genus *Hypophthalmus* has received no thorough treatment. Eigenmann & Eigenmann (1890) synonymised the six nominate species with *H. edentatus*, the type of the genus, stating 'There is little doubt but that the species have been based on the different stages of one species'. More recently, however, Roberts (1972:139) noted there are '. . . three very distinct species of *Hypophthalmus* in the Amazon'. In the most recent literature authors have recognised a second species named as *H. perporosus* Cope, 1878 (see Goulding, 1980; Carvalho, 1980*a*).

Although *Hypophthalmus* is a common commercial food fish in Amazonia (see Roberts, 1972: 140), its ecology is poorly studied (for accounts see Roberts, 1972; Meschkat, 1960; Goulding, 1980; Carvalho, 1980*a* & *b*). *Hypophthalmus* species are shoalers and filter-feed, chiefly on zooplankton. According to Carvalho (1980*b*), the larger proportion of ingested food of *H. edentatus* comprises cladocerans and copepods. Gut contents of specimens personally examined contain insect (Hymenoptera) leg and antennal fragments, and fragmented plant material (portions of leaves, stems, pollen cuticles and seed spikes). Carvalho (1980*b*) classifies *Hypophthalmus* as a pelagic zooplanktivore but perhaps, in view of the above catalogue of gut contents, it should more rightly be classed as a detrital filter-feeder. As in other detritivores, *Hypophthalmus* has a long, convoluted gut.

Only two papers deal with any detailed aspect of hypophthalmine anatomy. Wright (1885) described the skull and swimbladder connections. This paper, however, omits some important features and misinterprets others, omissions obviously due to limitations imposed by the use of dry skeletal material in which many delicate structures are lost or obliterated. Chardon (1968) also described the swimbladder and Weberian structure. His account and illustrations supplement those of Wright's. Roberts (1972) gives a more general account of *Hypophthalmus*, and includes a fairly detailed description of the gill arch structure and its likely mode of function.

List of genera examined

Where availability of material has permitted, the cranial anatomy of at least two species in each polytypic genus has been examined.

A = alizarin stained specimen, D = dry skeleton, S = alcohol preserved specimens (dissected).

Aelurichthys D
Ageniosus A, D, S
Amphilius A
Arius A, D, S
Aspredo S
Auchenipterus A, D, S
Bagrus A, D, S
Brachyplatystoma S
Branchioica A
Bunocephalus A
Callophysus S
Chaca D
Chaetostoma D
Chrysichthys A, D, S
Clarias A, D, S
Clarotes D, S
Cochliodon A
Cryptopterus D, S
Diplomystes D, S
Doras D
Eutropius D, S
Gagata D
Galeichthys D, S
Geneidens D
Glyptosternon D, S
Goldiella S
Helogenes A, D, S
Hemisorubim D, S
Heptapterus S
Hoplosternum D, S
Hypophthalmus A, D, S
Ictalurus A, D, S
Iheringichthys A, S
Leiocassis D
Liobagrus D
Loricaria D, S
Luciopimelodus D, S
Megalonema S
Mystus D
Nematogenys D, S
Notarius D
Osteogeniosus A
Ompok D, S
Oxydoras D
Pangasius S
Pangasianodon D
Parapimelodus S
Perugia S
Phyllonemus A
Pimelodina S
Pimelodus A, D, S
Platystomatichthys D
Plotosus D, S
Pseudauchenipterus S
Pseudobagrus A, D
Pseudocetopsis S
Pseudopimelodus D, S

Pterodoras D
Rhamdia D, S
Rhinodoras D
Schilbe A, D, S
Silurus D, S
Sorubim A, D, S
Sorubimichthys D, S
Synodontis S
Tandanus D, S
Trichomycterus A, S
Wallago D, S

Abbreviations used in the figures are given either in the relevant sections of the text, or in the figure captions.

Form and function in *Hypophthalmus* and comparison with other siluroids

The principal derived features of *Hypophthalmus* are listed below. The reasons for considering their derived nature are discussed under each character complex.

1. Body shape and pattern of the sensory canals and lateral line system.
2. The position of the eyes and arrangement of their musculature.
3. The hypertrophy of the facial, and the complexity of the hyoid musculature.
4. The particular morphology of the mouth and the articulation of the mandibular barbels with cartilaginous plates.
5. The reduction of the neurocranium and its complete ankylosis with the anterior vertebral complex.
6. The nature of the complex vertebrae, anterior placement of the Weberian ossicles, reduction plus encapsulation of the swimbladder, and displacement of the vagus nerve.
7. The extent of the gill openings and elongation of the branchial arch elements.
8. The elongation and modification of the hyoid arch.

Body shape, sensory canals and lateral line system (Figs 1 & 2)

Hypophthalmus has a deep and moderately compressed body with a sloped dorsal profile; the head is broad (30% of its length) with a subtriangular snout, the eyes are set at the same horizontal level as the mouth. There is a single pair of long maxillary barbels and two pairs of similarly long mandibular barbels. The gill opening extends almost as far forward as the mandibular symphysis.

The pectoral fin is narrowly triangular, its tip reaching beyond that of the small pelvic fin. The first ray of the pectoral fin is spinous and finely serrated along its outer margin. The anal fin is long with *c.* 62 branched rays, extending from the tip of the pelvic to below the adipose fin. The dorsal fin is short-based with I+6 rays; the small adipose fin lies midway between the dorsal fin and the origin of the forked caudal fin.

In life, *Hypophthalmus edentatus* has a silvery blue-green colour, the barbels are dark, the fins hyaline but with dusky tips to the pectorals, and a dark submarginal band on the anal fin.

The skin above the orbit is permeated with a network of canals which are denser and more ramified below the frontal margin than elsewhere (Fig. 2). The entry points to this network are through the pterotic and frontal sensory canal openings. Similar ramified patterns occur over the antero-dorsal and ventral portions of the operculum. Their respective connections are with the pterotic and preopercular canals.

The lateral line has dorsal and ventral branches. The longest dorsal branches are angled caudally at 45° to the main lateral line, some extending almost to the dorsal midline; shorter branches run cranially at a similar angle, thus forming a network (Fig. 1).

The longest ventral branches extend to the base of the anal fin where they curve caudally almost at a right angle (one or two branches curve anteriorly). Shorter, angled branches cross the upper part of the vertical lines and form the ventral counterpart of the dorsal network. The lateral line is bifurcated caudally, the longer arm, itself often sub-branched, extends to the 6th or 7th ray of the upper caudal lobe. The lower branch hardly reaches the base of the caudal fin and is absent in some specimens.

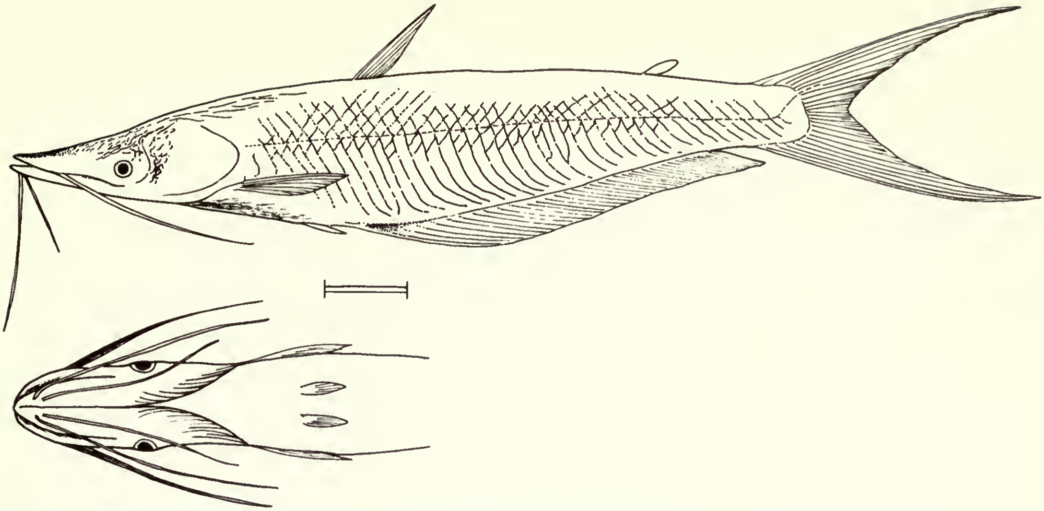

Fig. 1 *Hypophthalmus edentatus*; (upper) lateral view showing ramifying lateral line system; (lower) ventral view of head to show inferior position of the eye. Scale = 20 mm. Drawn from specimen BMNH 1925. 10.28:327.

The body shape of *Hypophthalmus* is like that described by Alexander (1965) for the African siluroid *Schilbe*. The salient features noted by Alexander of the schilbeid morphotype are a compressed trunk; long anal fin; short body cavity; reduced dorsal and adipose fins; deep epaxial musculature reaching well-forward on the cranium and the supraoccipital bearing a tall median crest onto which most of the dorsal musculature attaches. All these features apply to *Hypophthalmus* and occur also in Old-World siluroids (Siluridae e.g. *Ompok, Cryptopterus*; Schilbeidae, Pangasiidae) and the Neotropical Auchenipteridae (*Auchenipterus*) and Ageniosidae. As such it seems to be a morphotype independently derived in several lineages. Nonetheless, such a body shape is assumed to be a derived feature for each group in which occurs as it is always accompanied by some marked, but different modification of the swimbladder and, or, lateralis system.

Carvalho (1980*a*) found a high proportion of fat in *Hypophthalmus* (up to 26% body weight) which varied inversely to the total water content. This high fat content doubtless contributes to the attainment of neutral buoyancy and appears to be a correlate of a reduced swimbladder (see p. 28).

A highly ramified lateral line system similar to that in *Hypophthalmus* is also found in siluroids and pangasiids, but in no other taxon investigated do the lower branches extend so far ventrally or curve along the anal fin base. An orbital and opercular canal system like that of *Hypophthalmus* occurs similarly only in *Luciopimelodus*. A ramifying of canals are present on the cranial and postcranial regions of many siluroids, but generally as separate twiglets over the head and upper opercular region only. In the Ageneiosidae and Pimelodidae alone is there a lattice-like pattern aproaching that of *Hypophthalmus*. Furthermore, only in *Brachyplatystoma* and *Luciopimelodus* does such a system of canals cross the interoperculum. Other siluroids with a similar body shape to *Hypophthalmus* (e.g. *Pangasius, Schilbe, Ompok*) lack an intricate epidermal network.

Alexander (1965) observed that catfishes possessing the schilbeid morphotype (see above) were more pelagic than others, and accounted for the compressed, tapered body shape in terms of a specialised locomotion. A principal component of schilbeid locomotion is the ability to hover by inclining the body at a 45° angle to the surface. It has not been reported whether *Hypophthalmus* adopts a similar locomotory attitude. Neither is it clear whether *Hypophthalmus* should be classed as 'pelagic' for it seems that these fishes may make vertical migrations (Meschkat, 1960).

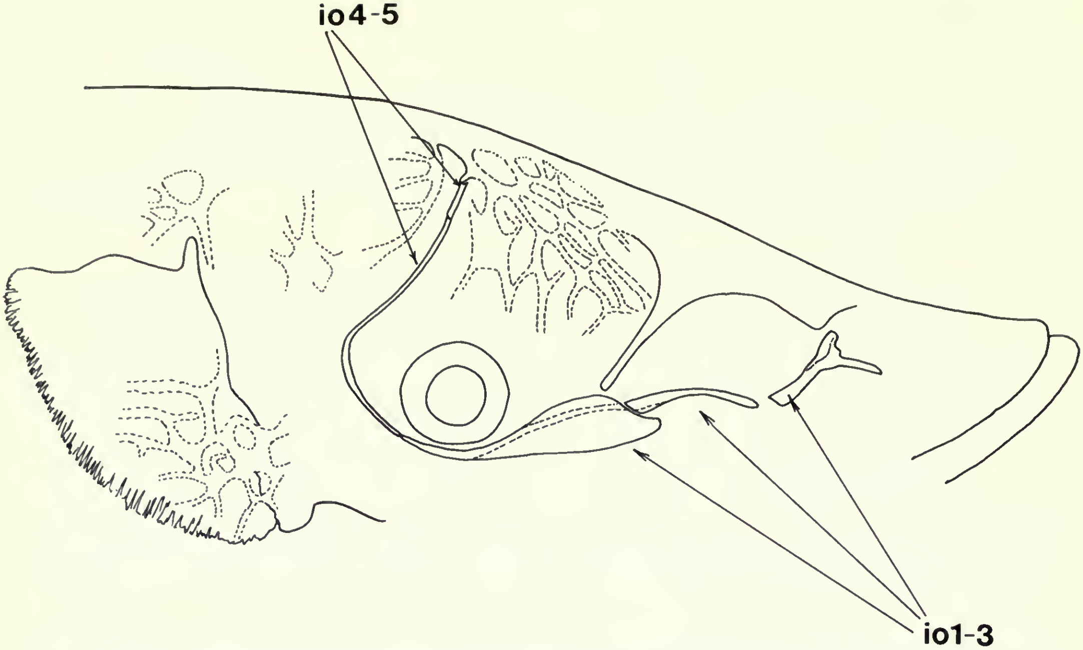

Fig. 2 *Hypophthalmus edentatus* lateral view of head showing sensory canal system and infraorbitals. Composite drawing.

The eye and infraorbital bones (Figs 2–4)

Two of the more noticeable features of *Hypophthalmus* are the position of the eye relative to other parts of the cranium, and the arrangement of the orbital muscles (Fig. 3).

The eye is of moderate size (12% of head length) and is situated on the ventral margin of the head at the same horizontal level as the mouth. When viewed ventrally the eyes appear as almost entirely inferior (Fig. 1).

The *eye muscles*, in their origins and position lateral to the adductor muscle complex, are unlike those of any other siluroid. The anterior muscles are long and strap-like. Both the *superior obliquus* (sob) and *inferior obliquus* (iob) have a common origin from a broad tendinous sheet that extends dorsally across the *adductor mandibulae* musculature to attach to the lateral margin of the frontal and to the lateral ethmoid. The optic nerve and those supplying the eye muscles all run parallel to one another within an almost vertical band of connective tissue. As in other siluroids the *superior obliquus* is innervated by the trochlear nerve (niv) and the *inferior obliquus* by a branch of the oculomotor (niii). The *rectus internus* (ri) arises from a thin tendinous strand that crosses the face of the adductor complex and runs between the *superior obliquus* and *inferior obliquus* muscles to attach to the anteromedial surface of the eyeball. The muscle is unnervated by a sub-branch of that branch of the oculomotor that feeds the *inferior obliquus.*

The posterior set of muscles, *rectus superior, r. inferior* and *r. externus* (Fig. 4, rs; rin; re) originate from a tendinous band which is strongly attached to the dermis. The former two muscles are innervated by branches of the oculomotor and the latter by the abducens (nvi).

The *optic nerve* (nii) is thick and exits from a slit-like foramen to loop over the adductor muscle complex and pass across its face which is grooved to accommodate it.

The *infraorbital bones* (io Fig. 2) are, with the exception of the 3rd, reduced to ossifications of the sensory canal. The 1st infraorbital is axe-shaped, the common morphology of this element amongst siluroids, the 2nd a slightly curved, cylindrical bone, the 3rd with an

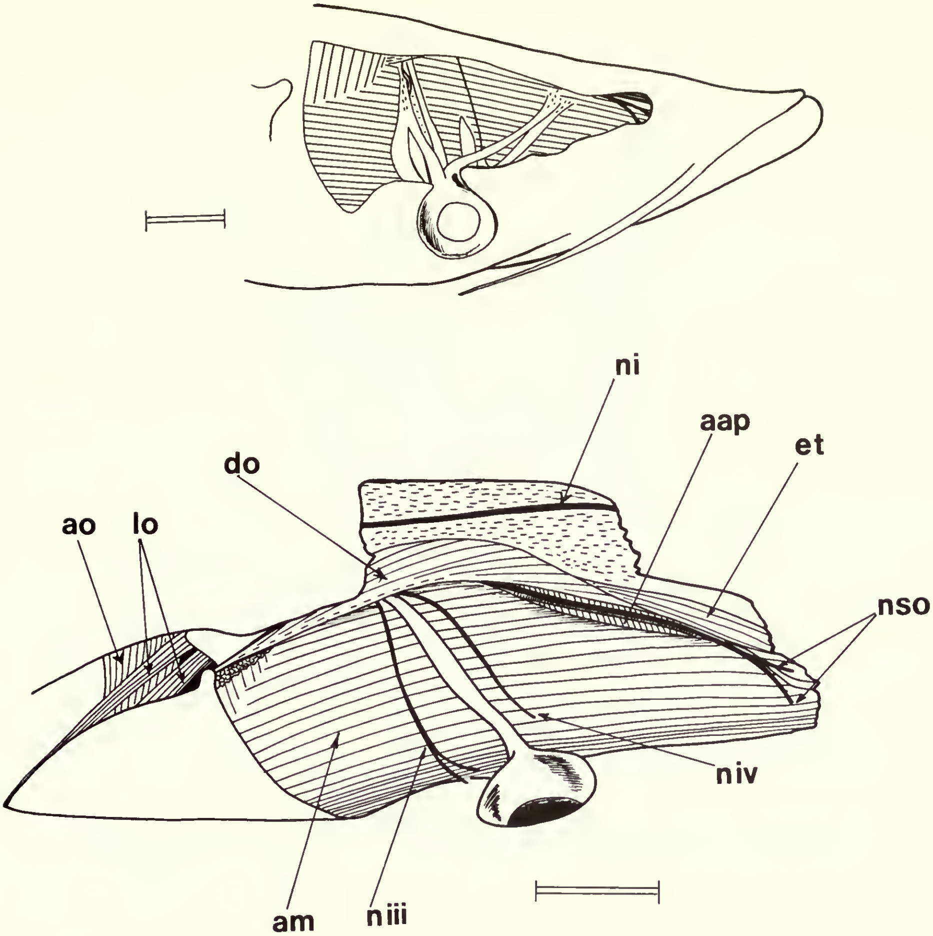

Fig. 3 *Hypophthalmus edentatus;* (upper) superficial dissection of the head showing position of the eye muscles in relation to the cheek musculature; (lower) dorsal view of orbital region (eye muscles removed) with frontal cut away to display the *dilatator operculi muscle* (do) and olfactory nerve (ni). Drawn from specimen BMNH 1976.6.18: 123–129. Scales = 5 mm. am = *adductor mandibulae*; nso = rami of supraorbital nerve trunk.

antero-ventral lamellae, its posterior, tubular portion lying beneath the orbit; the 4th, the largest of the series, curves dorso-posteriorly to beyond the border of the eye, then, at the upper level of the orbit, curves dorso-anteriorly to extend across the interspace between the orbit and the cranium; the 5th a small tubular bone connected to the pterotic.

Although unusual, the ventro-lateral position of the eye in *Hypophthalmus* is not unique amongst siluroids. It occurs similarly in *Ageniosus*, some *Auchenipterus* and *Pangasius* species. However, in all these taxa, the arrangement of the eye muscles is of the more normal teleost condition.

In both *Auchenipterus* and *Pangasius* the eye ball is cupped by the surrounding muscles, the posterior set passing into the optic foramen. *Ageniosus* is markedly similar to *Hypophthalmus* in the displacement of the optic nerve tract across the adductor muscle face. However, the musculature is extended laterally and there is a consequent orientation of the nerve tract, unlike the vertical course followed in *Hypophthalmus*. Furthermore, the eye muscle arrangement in *Ageniosus* is less modified in that the posterior muscles, although highly tendinous, join in a single cylindrical tract across the *adductor mandibulae* muscle.

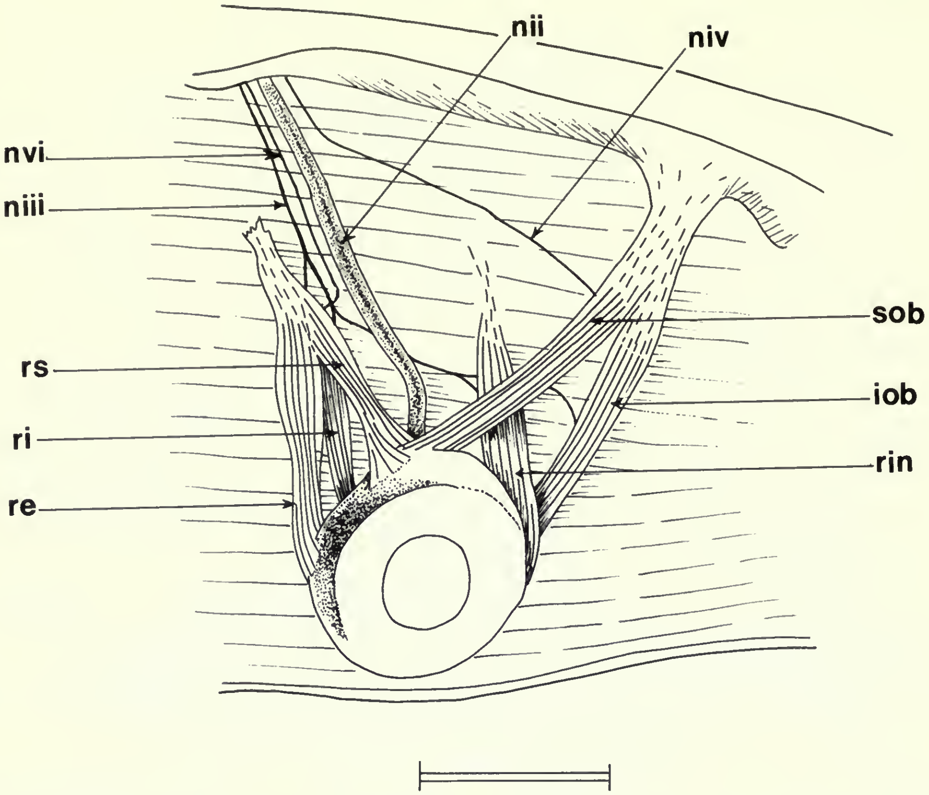

Fig. 4 *Hypophthalmus edentatus*; the eyeball, associated muscles and nerves (the upper skin reverted). Drawn from specimen BMNH 1976.6.18: 123–129. Scale = 5 mm.

Only in the pimelodid *Sorubimichthys* is there a muscle arrangement approaching that of *Hypophthalmus*. Although in the former genus the eye is superior in position and the posterior set of muscles are horizontally aligned, the anterior muscles originate from a tendinous band above the *extensor tentaculi* muscle (et Fig. 10).

The inferior orientation of the eyes in *Hypophthalmus* may provide a partially stereoscopic vision which would serve to alert the fish to an approaching predator. The degree of eye mobility in *Hypophthalmus* is unknown. The eye muscles are thinner, and appear 'weaker' than in the other taxa investigated, but their complete innervation suggests some degree of eye-ball movement.

According to Dullemeijer & Barel (1977) the eye in teleosts is a functionally dominant feature and in their opinion one with little positional plasticity. This is obviously not the case in *Hypophthalmus* where the eye has shifted ventrally from the usual siluroid superolateral position. In *Hypophthalmus* the position of the eye has apparently been 'dictated' by the form of the adductor muscle complex. This is in direct contrast to phytoplankton feeding percomorphs (Dullemeijer & Barel, 1977) where the eye has retained a superior position and consequently only a small area is available in which the adductor muscle can develop and operate.

In general, the eyes of siluroids appear to have a less dominant role than in other otophysans or indeed other teleosts. In many siluroids the trend has been for the eyes to have shifted into a superior position, taken to the extreme in some loricarioids (e.g. *Chaetostoma* and *Astroblepus*) where the orbits are separated by a minimal space.

Fink & Fink (1981) claim that the infraorbital series in siluroids is reduced to the canal bearing portion of the bone. Whilst this is true for the majority of taxa it does not hold for all; *Hypophthalmus* is one exception (see above). In the clariids, the posterior infraorbitals (includes 'supraorbital' *auctt.*) are greatly expanded.

The recognition of reduced infraorbitals and the absence of a supraorbital bone as synapomorphies linking siluroids with gymnotoids (Fink & Fink, 1981) is dubious. Such reduction and loss also occurs in cyprinoids (Cobitidae). An even more pertinent point is the differing arrangement of the infraorbitals in gymnotoids and siluroids—clearly shown by Fink & Fink (1981, fig. 7D–E). The anterior infraorbital bones of siluroids are always elongate and the 3rd extends someway past the orbit so that the posterior series curve dorso-anteriorly. In gymnotoids the 3rd infraorbital is a short bone and the posterior elements are directed diagonally in a dorso-posterior direction.

Cranial musculature (Figs 5–6)

Jaw and suspensorial muscles

When the eye, together with its muscles and the optic tract have been removed, the entire face of the fish is seen to be covered by an almost undifferentiated adductor muscle (Fig. 5). The orbital socket is indicated on the face of the muscle by a circular tendinous area, the optic tract by a vertical groove (otf, Fig. 5). Dorso-posteriorly, lateral fibres of the *levator arcus palatini* muscle (lap) adhere to the adductor's surface, and a more medial section of the levator is indicated by a longitudinal division of the adductor.

The posterior origin of the *adductor mandibulae* is from the lateral and antero-medial faces of the hyomandibula. Anteriorly, at the articulation of the lower jaw, there is a myocomma and the adductor can be differentiated into a number of segments. The upper, outer portion curves inward, its anterior border being tightly attached to the thick mandibular nerve tract (nvmd) which follows the muscles contour as it passes medially to

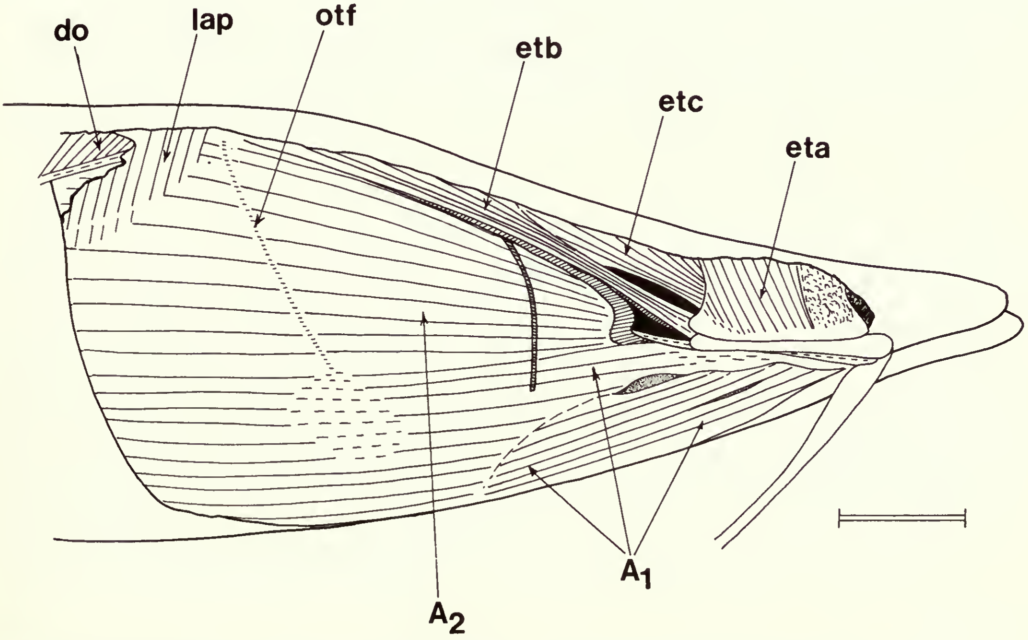

Fig. 5 *Hypophthalmus edentatus*; superficial head musculature. Drawn from specimen BMNH 1976.6.18: 123–9. Scale = 5 mm.

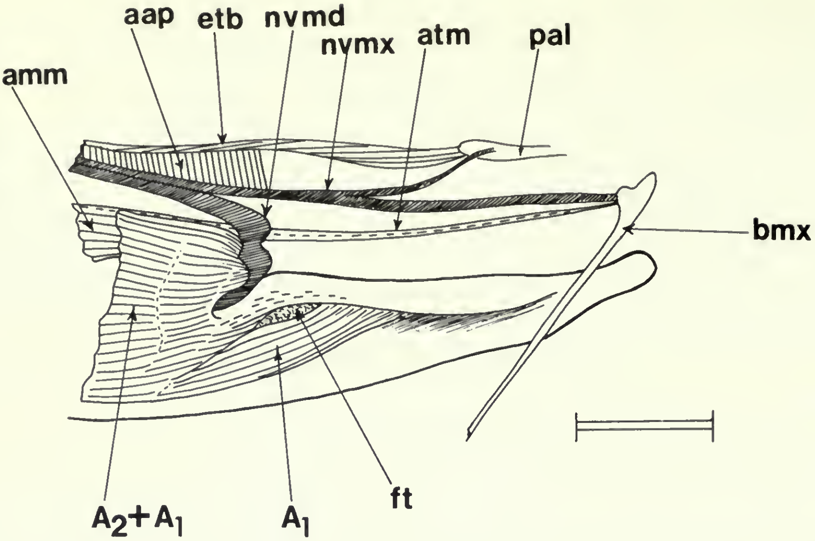

Fig. 6 *Hypophthalmus edentatus*; lower jaw musculature. The palatine and extensor muscle have been raised. In relaxed position the tendon (atm) passes between the rami of the maxillaris nerve (nvmx). Drawn from specimen BMNH 1976.6.18: 123. Scale = 3 mm.

attach to the inner face of the lower jaw. From its insertion this part of the muscle is regarded as section A_2 (Fig. 6). There is no recognisable A_w, A_2 inserting *via* a broad tendon stretching across the medial face of the *adductor mandibulae* mass.

The antero-ventral part of the muscle lying lateral to the mandibularis nerve trunk is divisible into an upper bundle of fibres inserting into the lip tissue covering the coronoid process, and a ventral section inserting partially into labial tissue and partially on the lateral face of the dentary (A_1, Fig. 5). When the superficial layer of the dorsal part of A_1 is removed, a medial layer is found to be continuous with A_2 (amm, Fig. 6); this division appears to be homologous with the *retractor tentaculi* (see below). The posterior border of the ventral part of A_1 is marked by a myocomma. A short, pinnate bundle of fibres stems from the antero-medial face of the adductor complex and inserts into a long tendon (atm, Fig. 6). The tendon passes between the maxillary and mandibular branches of the trigeminal nerve to insert on the maxilla at the base of the barbel.

There is no discrete medial division of the main body of the *adductor mandibulae*, only posteriorly is there a separation by a medial sheet of the *levator arcus palatini* muscle (see above), but the fibres of both muscles intermesh.

The central portion of the *adductor arcus palatini* extends between the parasphenoid and the dorsal border of the pterygoid bones (aap, Fig. 6). A separate, posterior portion runs from the parasphenoid to the medial face of the hyomandibula, and is identified as the *adductor hyomandibulae*. The anterior part of the *adductor arcus palatini* is divisible into three sections which together comprise the *extensor tentaculi*. The antero-dorsal part of this muscle covers the lateral ethmoid and attaches to the posterior half of the palatine (eta, Fig. 5). The postero-medial part originates as two separate sections from the central region of the *adductor arcus palatini*. The longer, postero-medial section runs forward at an oblique angle to insert on the postero-medial portion of the palatine (etb, Fig. 5). The shorter, medial portion runs antero-dorsally to insert on the antero-medial part of the palatine (etc, Fig. 5).

Innervation

Two thick nerve tracts stem from the trigeminofacial ganglion and exit from a single prootic foramen. The supraorbital trunk diverges immediately. The infraorbital trunk is of great

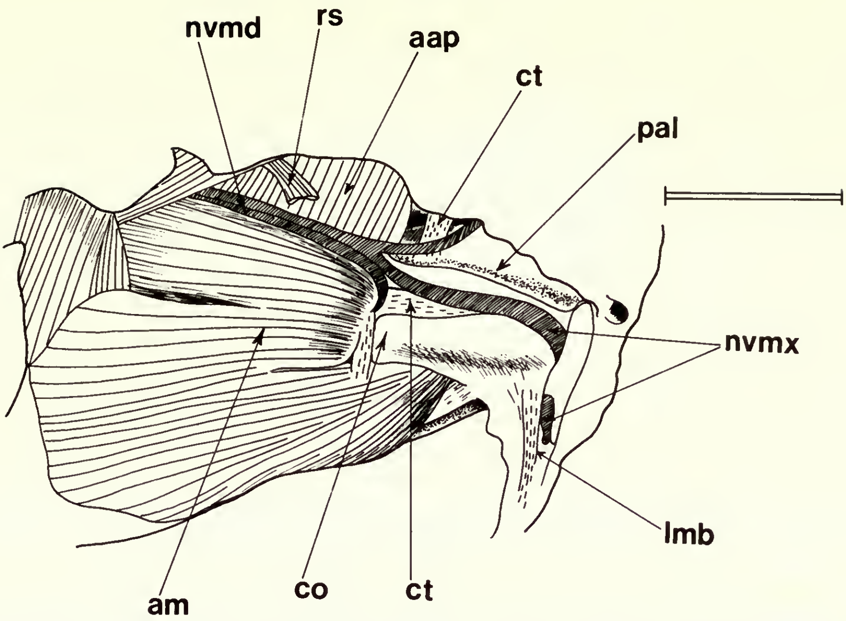

Fig. 7 *Nematogenys inermis*; dorso-lateral view of cheek musculature. Drawn from specimen BMNH 1883.11.27: 45–48. Scale = 10 mm. co = coronoid process; ct = connective tissue; lmb = ligament connecting maxillary barbel with mandible.

thickness, and above the jaw articulation it divides into the buccal and maxillo-mandibular rami which pass, respectively into the root of the maxillary barbel and the lower jaw. (Fig. 6). The buccal ramas gives off a branch to the *adductor arcus palatini* before bifurcating into an outer branch serving the area of the *extensor tentaculi* muscle around the palatine, and an inner branch which enters the base of the maxillary barbel. The mandibular ramus (nvmd) curves round the anterior border of the adductor muscle complex, sending off short branches into the musculature (Fig. 6). The trunk passes across the inner face of the dentary to run inside the length of the bone before terminating in a bifurcation, each branch of which enters its respective barbel (Figs 7 & 14).

Jaw and suspensorial muscles in other siluroids

It is generally accepted (see Winterbottom, 1974) that in teleosts the section of the *adductor mandibulae* termed A_1 is that which forms the outer, or dorsal muscle segment inserting on the maxilla. Section A_2 is that which lies medially and, or, ventrally to A_1, and inserts on the lower jaw; the part of it which covers the medial face of the dentary is termed A_w. Further divisions (A_2a, A_3 etc) are those successively medial to A_1 and A_2 and which insert onto the inner face of the lower jaw.

In siluroids, this seemingly straightforward nomenclature has become somewhat confused through the presence of a muscle, serving the base of the maxillary barbel, known as the *retractor tentaculi*, often referred to as the *adductor tentaculi* or *protractor maxillae*; see Winterbottom, 1974 for synonymy. The fact that this muscle inserts on the maxilla but stems from the medial aspect of the *adductor mandibulae* has led to its being homologised with various sections of the adductor complex.

Takahasi (1925) thought that because of its maxillary insertion it was synonymous with division A_1, a hypothesis followed by Edgeworth (1935). McMurrich (1884*b*) and Lubosch (1938) considered the *retractor tentaculi* to be an *inner* division of the adductor. Eaton (1948) agreed, in referring to *Ictalurus* thus . . .'From the fact that a stout ligament runs from the base of the adductor tendon back and downward to join the ligamentous sheath of the

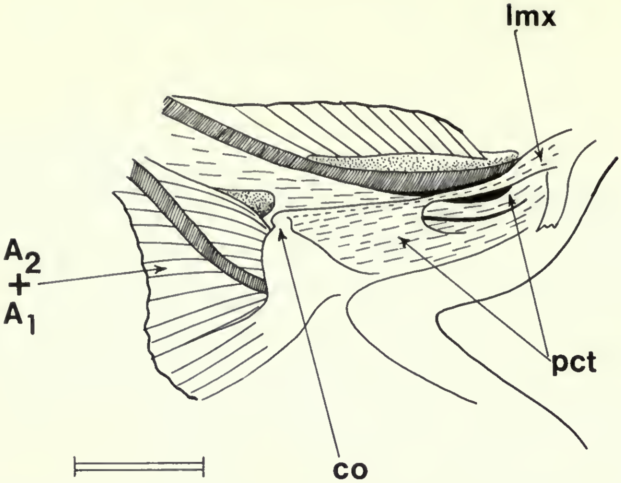

Fig. 8 *Callophysus macropterus*; lateral view of muscular and ligamentous connections to the upper and lower jaws. Drawn from specimen BMNH 1913.7.30: 20–22. Scale = 5 mm. lmx = maxillary-mandibular 'ligament'; pct = palato-pterygoid connective tissue.

quadrato-articular joint, I would infer that the muscle has simply taken hold, as it were, of the primitive ligament which runs, in such fishes as *Amia calva*, from the articular to the maxillary. Thus, the ligament has now become in large part a muscle tendon. . .'

Alexander (1965) concurs with Eaton, believing that the *retractor tentaculi* (the *adductor tentaculi* of Alexander) is derived from '. . .A_3 rather than A_1'.

From the arrangement in siluroid taxa I have investigated, it appears that these latter authors are probably correct in assuming that the *retractor tentaculi* is part of the inner adductor series and that its attachment with the upper jaw is a *de novo* development. The possible evolutionary development of the *retractor tentaculi* as suggested by Eaton (1948) and Alexander (1965) can be amplified by the following observations.

The presumed plesiomorph condition of the *adductor mandibulae* muscle in siluroids is where divisions of the muscle are not well-differentiated and insertion is entirely, or almost entirely, on the lower jaw. *Diplomystes* and *Nematogenys* (Fig. 7) illustrate this condition where the lower, outer part inserts musculously on the lower jaw (anguloarticular). An upper, inner division can be distinguished by its attachment, anteriorly, to the lower part by a broad vertical tendon which covers the postero-dorsal rim of the lower jaw. Stemming from the antero-medial surface of this muscle, and extending across the dorsal surface of the mandible is a thick sheet of connective tissue (ct). This sheet bifurcates, the upper strand attaching to the posterior face of the maxilla, the lower to the distal portion of the maxilla where it forms a sheath around the maxillary barbel.

In *Callophysus*, Pimelodidae, a continuous sheet of tissue extends medially from the dentary to the anterior pterygoid process (pct, Fig. 8). That area of tissue covering the coronoid process is thickened and, anteriorly, is separated from the main sheet so forming a distinct 'ligament' running to the base of the maxillary barbel (lmx, Fig. 8).

A similar arrangement of the 'ligament' is present in *Tandanus* and *Plotosus*. Alexander (1965), following Takahasi (1925), states that the deepest part of the *adductor mandibulae* inserts on the articular-maxillary ligament. This is, however, incorrect. A strong ligament does indeed stretch from the posterior aspect of the maxilla to the coronoid process of the dentary, and appears to be homologous with the partially differentiated 'ligament' described above in *Callophysus*, but no muscle inserts on it (lmx, Fig. 9). The outer portion of the *adductor mandibulae* in *Tandanus* and *Plotosus* inserts on the lower jaw *medial* to the ligament. The inner sections of the adductor, be they interpreted as A_2 or A_3, insert on the medial face of the anguloarticular (Fig. 9).

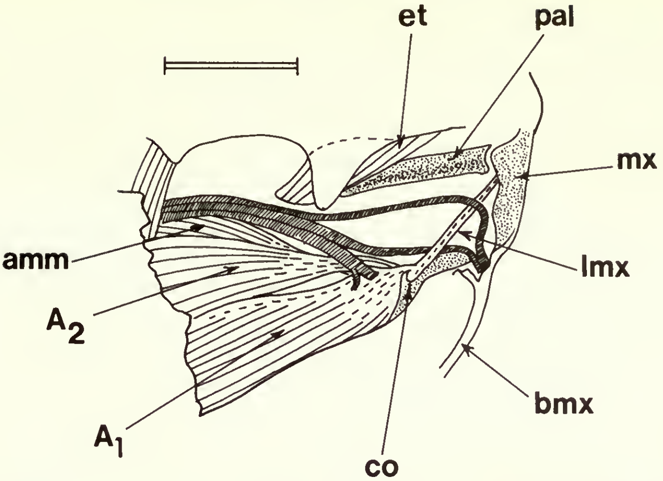

Fig. 9 *Tandanus tandanus*; dorso-lateral view of jaw muscle attachments. Drawn from specimen BMNH 1871.2.10: 4–6. Scale = 10 mm.

Kesteven (1943) also erroneously identified a *retractor tentaculi*, his protractor maxillae, in *Tandanus*. He states that the muscle '. . .arises from the side of the skull above the anterior attachment of the palatal arch. . .' to insert on the maxilla '. . .enswathing the posterior end of the bone.' I find no such muscle in *Tandanus tandanus* (Fig. 9) nor in *Plotosus plotosus* and must presume Kesteven misidentified part of the *extensor tenatculi* or else did not entirely dissect the connective tissue enswathing the maxilla.

In the pimelodids *Pimelodus* and *Iheringichthys* and the bagrid *Clarotes* a distinct ligament connects the base of the maxillary barbel with the coronoid process of the dentary. However, the ligament then courses posteriorly from the coronoid process to the fascia of the medial section of the *adductor mandibulae*. A further modification of this condition occurs in one group of pimelodids, *Parapimelodus* and *Pimelodus maculatus*, whereby there are two distinct ligaments extending from the base of the barbel, the outer attaching to the coronoid process and the medial one to the pterygoid process. In none of these taxa does the musculature attach to the ligaments.

In *Megalonema*, Pimelodidae, the maxillo-articular ligament bifrucates posteriorly, the inner branch becoming continuous with the tendon of the medial segment of the adductor muscle complex. The outer ligament is, however, still connected with the lower jaw. In *Sorubimichthys*, Pimelodidae, a distinct ligament connects the maxilla with the coronoid process of the dentary. However, the ligament is tightly attached along the length of the upper jaw (premaxilla) by connective tissue. A branch of the mandibularis nerve runs into the tissue joining the upper and lower jaws (Fig. 10).

These examples serve to illustrate the probable pattern involved in the evolution of the *retractor tentaculi*. The hypothesised stages of this process are; (1) the palato-mandibular connective tissue becomes differentiated to form a stout, free ligament connecting the maxilla with the posterior part of the lower jaw, (2) medial fibres of the *adductor mandibulae* become associated with the maxillo-palatine part of the palato-mandibular tissues, (3) the connective tissue becomes further differentiated and tendinously links a discrete medial section of the *adductor mandibulae* with the root of the maxillary barbel.

The basic conditions for the development of the *retractor tentaculi* are present in several members of the Pimelodidae, Bagridae and Plotosidae and it seems very likely that the muscle has been derived independently in several lineages. Various apomorphic conditions of the muscle can be recognised as for example in some pimelodids such as *Rhamdia* where the anterior segment is attached to the orbitosphenoid *via* a bifurcated tendon.

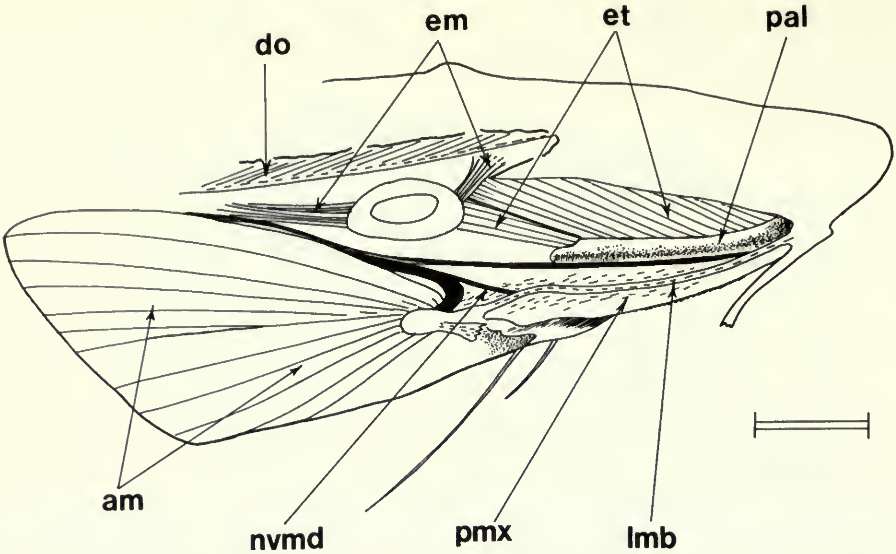

Fig. 10 *Sorubimichthys planiceps*; dorso-lateral view of superficial jaw musculature. Drawn from specimen BMNH 1977.5.24: 12. Scale = 5 mm. em = eye musculature, lmb = maxillary barbel-mandibular ligament.

If the *adductor mandibulae* muscles of siluroids are compared with those of other otophysans, their arrangement is seen to correspond most closely to that of characoids, where section A_1 also inserts on the dentary. Vari (1979: 317) considered that a lower jaw insertion for the outer part of the adductor represented the plesiomorph condition. In characoids a strong, well-differentiated maxillary-mandibular ligament is present and often the dorso-lateral fibres of A_1 attach to this ligament. Vari (1979) notes that incorporation of the ligament into the tendon of A_1 is a derived condition in distichodontid characoids.

In cyprinoids the section A_1 never inserts on the lower jaw and there is no maxillary-mandibular ligament.

In gymnotids there is a maxillary-mandibular ligament and in *Gymnotus* a few fibres of the outer part of the adductor muscle insert on this ligament; the remainder of the muscle inserts onto the outer face of the lower jaw, as in siluroids. However, this is not the case in *Sternopygus, Eigenmannia* and *Rhamphichthys* the only other gymnotid taxa examined, where the outer segment of the adductor attaches to the 1st infraorbital in *Sternopygus* and *Eigenmannia*, and to both the 1st infraorbital and the maxilla in *Rhamphichthys*.

Two hypotheses are available to account for the arrangement of the outer adductor muscles in siluroids. 1. That the insertion on the lower jaw is plesiomorphic and the ligamentous strand connecting the maxilla with the dentary is homologous with that similar ligament in characoids. 2. That insertion on the lower jaw is a derived feature brought about by regression of the maxilla and the loss of its intimate connection with the lower jaw. In effect, a regression of the cyprinoid condition.

Fink & Fink (1981) favour the second hypothesis stating . . .'The conditions in some characiformes and in siluriformes are hypothesised to be secondary reductions from a primitive attachment to the maxilla.' Although Fink & Fink refer to *some* Characiformes, the outer element of the *adductor mandibulae* attaches to the lower jaw in the *majority* of characiform taxa. In those siluroids where the *adductor mandibulae* inserts on the upper jaw, Loricariidae, Astroblepidae, it is to the *premaxilla* and the muscles involved are derivatives of the *medial* and not the *outer* parts of the adductor complex (Howes, in press). Only in the Callichthyidae is there an insertion of A_1 on to the maxilla, and this appears to be a derived condition associated with the maxillary-ethmoid joint (Howes, in press). In view of these observations I would regard a lower jaw insertion of the *adductor madibulae* A_1 in siluroids as the plesiomorph condition. The use of this character by Fink & Fink (1981) uniting the siluroids and the gymnotoids cannot be upheld, as in some (?the majority) of gymnotoids, the outer part of the adductor muscle inserts on the 1st infraorbital and not the lower jaw (see above).

The opercular muscles (Figs 3 & 5)

The *dilatator operculi* (do, Figs 3 & 5) is an exceptionally long muscle having its area of origin anterior to the orbit, the fibres adhering to, and covered by, the ventral margin of the frontal. Posteriorly, above the optic tract, the muscle is exposed before becoming tendinous and passing between the *adductor mandibulae* and the medial section of the *levator arcus palatini*. The long insertion tendon attaches to the antero-dorsal process of the operculum.

The *levator operculi* (lo Fig. 3) comprises two thin segments, an upper one arising from the postero-dorsal face of the hyomandibula and inserting on the postero-dorsal margin of the operculum, and a medial one originating from the pterotic and inserting on the antero-medial face of the operculum.

The *adductor operculi* (ao Fig. 3) originates from a fossa indenting the pterotic, exoccipital and 'posttemporal'. It inserts on the dorso-medial face of the operculum.

The hyoid muscles (Figs 11 & 12)

The ventral head muscles have a complex arrangement with much integration of the various segments.

The ventral layer exhibits two groups of muscles; those in which the fibre direction is toward the midline and those in which it runs antero-laterally.

The largest element (hma, Fig. 11A), belonging to the latter group, occupies half the lateral aspect of the lower jaw. Its fibres run at an oblique angle from the anterohyal to the dentary; anteriorly they change direction to run almost longitudinally. The outermost fibres insert onto the forepart of the dentary whilst the remainder turn inward as a separate bundle and are incorporated into the medial section (hmb, Fig. 11A). This medial part of the muscle also originates from the anterior part of the anterohyal. The muscle is formed from two sheets. The ventral, medial portion (hmb1, Fig. 11A) curves antero-medially, its outer fibres inserting on the cartilaginous plate of the inner mandibular barbel, its inner fibres meeting those of its antimere at a midline raphe. The lateral portion (hmb2, Fig. 11A) runs anteriorly to insert on a tendinous pad covering the cartilaginous base of the outer mandibular barbel (see below). A separate bundle of fibres insert into the base of the barbel. The medial fibres of hmb2 overlie the lateral aspect of hmb1, but at the midline both muscle-layers meet at a raphe.

Covering the branchiostegal rays and extending forward as a thin, longitudinally fibred segment is muscle hmc (Fig. 11A). Anteriorly it joins an aponeurosis into which hmb1 inserts; medially it joins its partner at a midline raphe. Extending forward from the aponeurosis is a discrete bundle of fibres that attaches to the base of the inner mandibular barbel (hmd, Fig. 11A).

The large muscle (hma) is considered, from its disposition and innervation by the ramus hyoideus VII to be the posterior *protractor hyoidei*. The inner divisions (hmb1 and hmb2 are also innervated by branches of the r. hyoideus VII and appear to be anterior parts of the *protractor hyoidei*. The small muscle slip attaching to the outer mandibular barbel is merely a continuation of the dorsal portion of this muscle and can be identified with that element named by Singh (1967) as a *retractor tentaculi*, not to be confused with his use of this name also for the facial muscle. The longitudinal muscle (hmc) is the *hyohyoidei adductores*. It is unclear, however, if the small bundle of fibres (hmd) running from its anterior aponeurosis to the inner mandibular barbel is indeed part of this muscle or whether it is derived from the *protractor hyoidei*. This small barbel muscle should also be identified with Singh's (1967) *retractor tentaculi*, which Winterbottom (1974) considered to be homologous with the

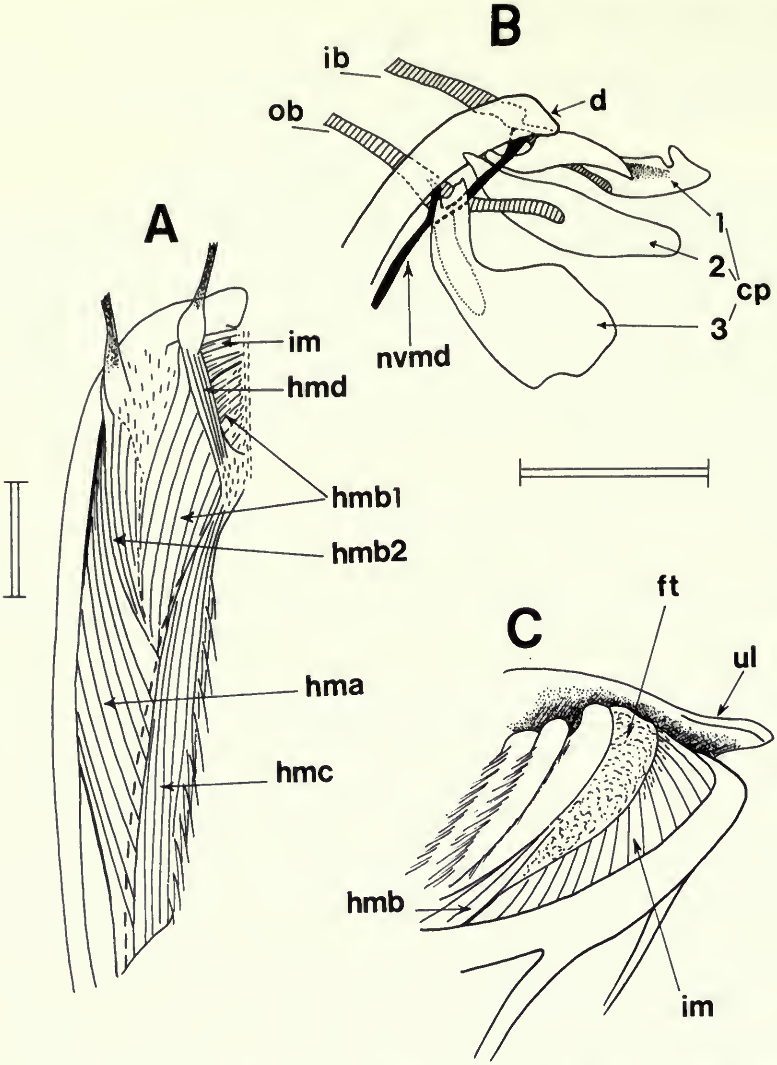

Fig. 11 *Hypophthalmus edentatus*; A, ventral view of hyoid musculature (right side); B, dorsomedial view of mandibular barbel supporting elements (left side). Thick dashed lines = nerve path, thin-dashes and dots = outline of barbel root; C, lateral view of mouth, upper lip cut sagittally. Drawn from specimens BMNH 1972.7.27: 675–678 & 1976.6.18: 123. Scales = 5 mm ul = upper lip.

retractor hyoidei. Ghiot (1978) illustrated in *Pimelodus* five separate muscles controlling the mandibular barbels of which he ascribed origin to 'differentiation of the hyoid protractor'.

The *intermandibularis* (im, Figs 11A & C) forms the anterior transverse muscular floor of the mouth. It is divided medially and each segment is attached to its respective cartilaginous plate which serves to support the barbel (see below). In the midline, each half of the muscle joins in a raphe which, in turn, is attached by strong connective tissue to an overlying collar of fatty tissue (ft, Fig. 11C). This collar encircles the leading edge of the antero- and dorsohyals and covers the basihyal.

Only in some pimelodid taxa is there such a complex arrangement of the hyoid musculature as in *Hypophthalmus*. In *Pimelodus, Sorubim* and *Pseudoplatystoma* the *protractor hyoidei* is complexly aponeurotic, and for its greater part is attached to the large

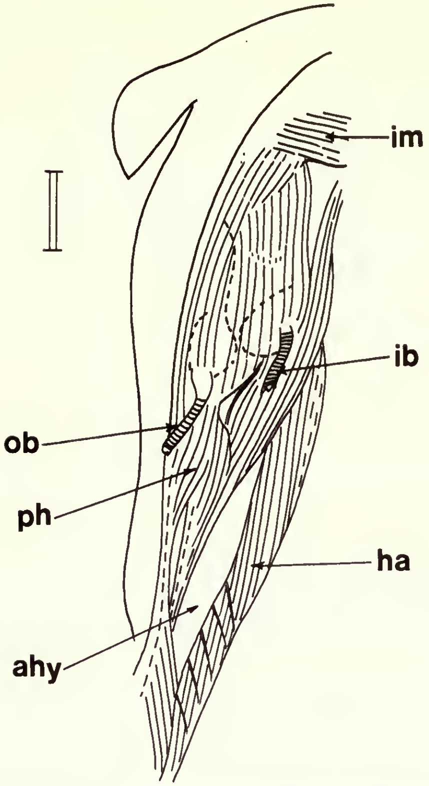

Fig. 12 *Sorubim lima*; ventral view of hyoid musculature (dashed lines = outlines of barbel supporting plates. Drawn from specimen BMNH 1969.7.15.26. Scale = 5 mm. ib, ob = inner and outer mandibular barbels.

cartilaginous plates supporting the bases of the barbels (Fig. 12). Ghiot (1978) distinguished in *Pimelodus clarias* five separate sections of what he termed the superior hyoidian protractor muscle in addition to separate lateral and medial divisions. The complexity of the hyoid musculature with separate mandibular barbel muscles attached to basal cartilages appears to be derived for at least one group of pimelodids and the Hypophthalmidae. The usual condition in siluroids is for the mandibular barbels to be 'embedded' within the *protractor hyoidei*, with bundles of fibres inserting on the anterior and posterior bases of the barbels and performing the function of retractors and protractors. This arrangement of hyoid musculature is illustrated by Singh (1967) in Bagridae and Winterbottom (1974, fig. 12) in Ictaluridae.

Unlike other otophysans, the siluroids exhibit considerable variability in the morphology of the hyoid musculature. A comparative study of these various arrangements appears to offer a fruitful field of potential synapomorphies.

The snout and jaws (figs 11–15)

Ramsay Wright's (1885) description of the snout region in *Hypophthalmus* can hardly be bettered and the following account is merely a supplement.

The entire *ethmoid region* is of papyraceous bone interspersed with cartilaginous strips (ec). Such cartilaginous areas separate the ethmoid (eth) from the lateral ethmoids and are bridged by the spine-like *nasal bones* (na, Fig. 13A). It is not possible to determine whether the ethmoid bone is a supra- or a mesethmoid. That it is so thin, and its lateral and posterior

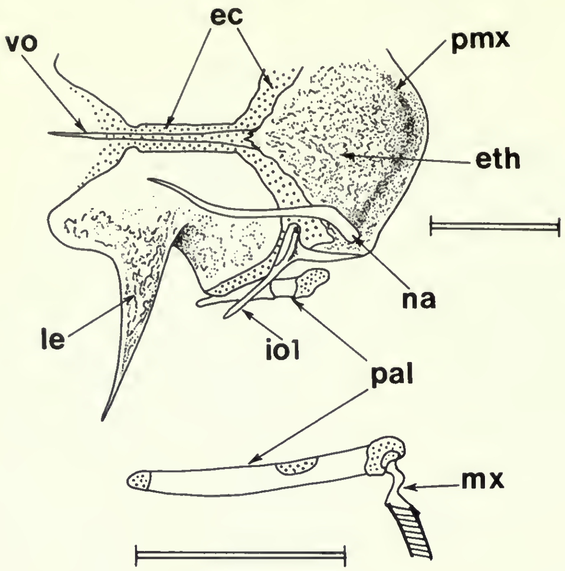

Fig. 13 *Hypophthalmus edentatus*; (upper) dorsal view of ethmoid region, (lower) palatine-maxillary articulation. Scales = 5 mm. Drawn from specimen BMNH 1972.7.27: 675–678.

margins grade into cartilage suggest that it is a single element and is entirely mesethmoidal in origin.

The *lateral ethmoid* (le, Fig. 13) has a wide anterior surface with a convex antero-lateral margin; postero-laterally its border is produced into a long, ventrally directed spine which almost meets the third infraorbital. The medial border of each lateral ethmoid abuts the midline mesethmoidal cartilage. The *vomer* is needle-like, its head slightly broadened and resting below the ethmoid (v, Fig. 13).

The nostril is bordered medially and laterally by the anterior arm of the bifurcated 1st infraorbital.

The edentulous *premaxillaries* (pmx, Fig. 13) are barely identifiable as separate elements, being fused with the ethmoid and distinguishable only by their denser ossification. They are so firmly united at the symphysis that even under a magnification of 50× a suture is not visible in alizarin preparations. The *maxilla* is a small, well-ossified, flattened and hook-shaped bone (mx, Fig. 13). The blade of the hook supports the barbel (bmx), its base is rounded and articulates withe the cartilaginous tip of the palatine.

The rod-like *palatine* (pal) is ossified, apart from its anterior and posterior tips and a small medial disc at about its midpoint (Fig. 13). This disc articulates with the lateral border of the lateral ethmoid.

Like the upper jaw, the lower jaw is also edentulous. The dentary (d) contributes to half the length of the mandible and is strongly sutured to the anguloarticular (aa).

The coronoid process is formed largely by a dorsal extension of the Meckelian cartilage (com, Fig. 14). The horizontal segment of this cartilage extends anteriorly along the medial face of the dentary and also has a slight posterior extension. The mandibularis nerve passes across the medial face of the upright part of the cartilage and then between the horizontal segment and the dentary wall. The nerve trunk continues along the ventral rim of the dentary and then bifurcates, each ramus inserting into the base of a corresponding mandibular barbel. A separate rod-like cartilaginous element lies antero-dorsally to the coronoid cartilage (cr, Fig. 14). Its distal tip is forked, and attaches to the lateral fold of thick labial tissue. The cartilage is mobile. When the jaws are abducted, and the labial tissue made taught, the cartilaginous rod rises to an acute angle.

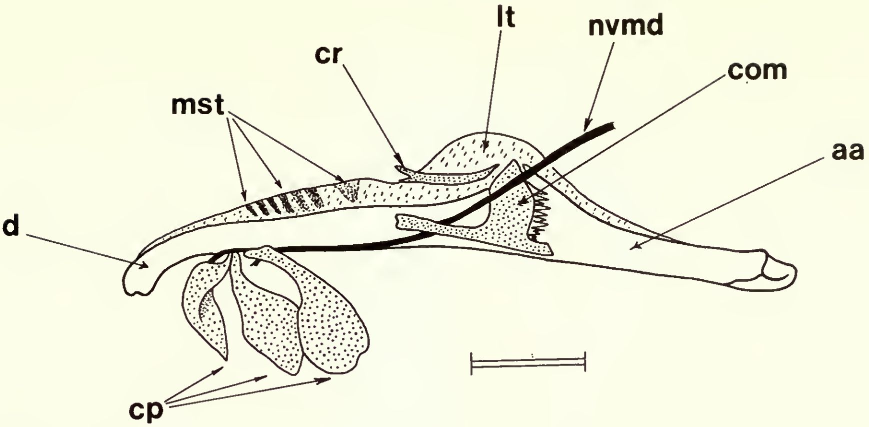

Fig. 14 *Hypophthalmus edentatus*, lower jaw (right) in medial view. Drawn from specimen BMNH 1972.7.27: 675–678. Scale = 5 cm. com = coronoid process of Meckelian cartilage; lt = labial tissue.

The *barbels* are supported on three cartilaginous plates (cp, Figs 11B & 14). The first, i.e. the element closest to the jaw symphysis, is the most complex. Its flat proximal tip attaches to the dentary rim and is curved where the mandibularis branch passes between it and the dentary. The cartilage extends dorso-posteriorly as an open cylinder, its distal tip providing the insertion site for the *intermandibularis* muscle. The root of the inner barbel (ib) bifurcates, one part ending as a short hook on the outer part of the cartilage, the other extending along the outer side of the cylindrical section. The two inner plates are irregularly shaped. The 2nd, middle, plate contacts the symphysial plate dorsally; the 3rd, outer, is notched at its articulation with the dentary thus allowing transmission of the mandibular nerve branch to the outer barbel (ob). As with the inner barbel the outer one is also bifurcated, its thicker leg attaching to the 3rd plate, its inner, thinner leg becoming 'cartilaginous' and extending posteriorly to join the centre of the 2nd cartilaginous plate.

Uniquely amongst siluroids, the anterior portions of the ceratobranchials enter the floor of the mouth and are curved upward, with the result that the basihyal is raised to the level of the roof of the mouth and the dorsohyals touch the underside of the ethmoid. The elevation of the floor of the mouth appears to be accomplished by the upward rotation of the medial cartilaginous plates supporting the *intermandibularis* muscle (see p. 16). The *intermandibularis* thus forms a hillock against the underside of the ethmoid and the thin upper lip tightly embraces the lower jaw when the mouth closes. The pressure created by the floor rising against the roof of the mouth serves to force water through the mesh-like gill-rakers which filter out particulate material. The length of the gill openings presumably allows a high volume of water to pass rapidly over the gill-arches.

The skin covering the dentary contains 7–8 transverse tubes (mst, Fig. 14) filled with a jelly-like substance staining intensely with the mucus-specific stain alcian blue. Of the taxa examined *Iheringichthys* has a similar jelly-like material in the lower lip, but it is concentrated in ampullae in the tissue close to the jaw symphysis and not arranged in widely spaced rows. Gelinek (1978) has described ampullary organs in the epidermis of *Sorubim*. He found them to be densely grouped in the labial tissue of the upper jaw and noted their structural similarity to those organs in *Plotosus*. Gelinek observed the similarities between these organs to those of gymnotids and mormyrids, thus hypothesising a similar function, namely electroreception.

The snout and jaws in other siluroids

The presumed plesiomorph condition of the ethmoid in siluroids is that which occurs in

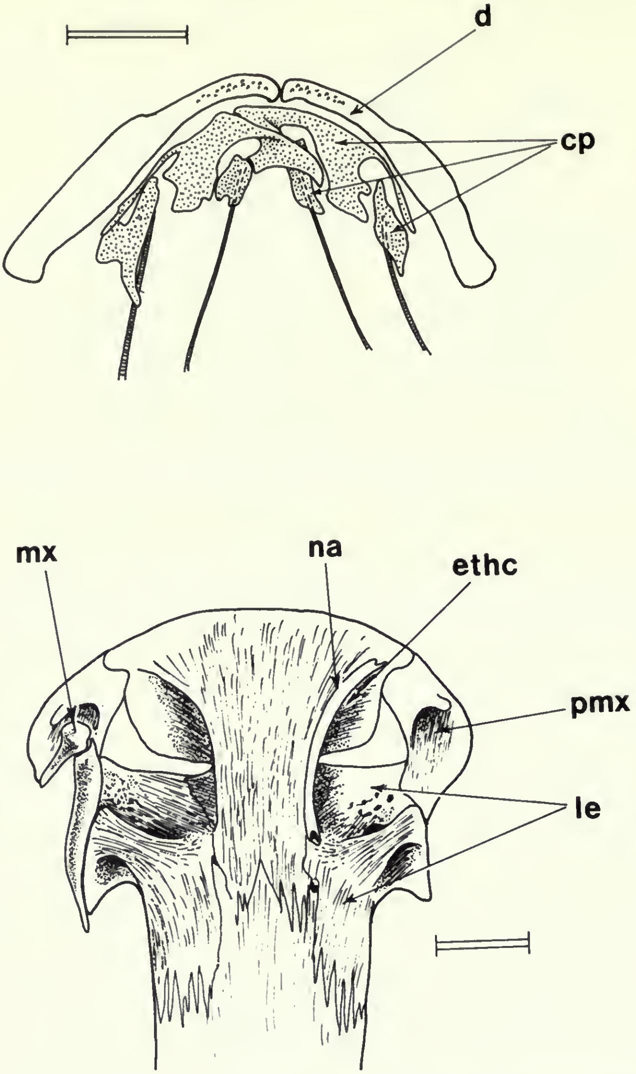

Fig. 15 Upper, *Iheringichthys labrosus*, ventral view of mandibular barbel supporting elements. Specimen BMNH 1934.8.20: 70–72. Scale = 2 mm. Lower, *Luciopimelodus pati*, dorsal view of ethmoid region. Specimen BMNH 1878.5.16: 30 (dry skeleton). Scale = 3 mm. d = dentary.

many taxa belonging to the Diplomystidae, Trichomycteridae, Bagridae, Ictaluridae, Pimelodidae, Mochokidae, Plotosidae and Loricariidae, here the ethmoid is elongate and T-shaped and often with a median anterior notch (see Fink & Fink, 1981). Howes (1980) mistakenly considered this type of ethmoid in Mochokidae as apomorphic.

In its presumed plesiomorph condition, the siluroid lateral ethmoid is triangular, closely united with the parasphenoid ventromedially and with the orbitosphenoid posteriorly.

The expanded and poorly ossified ethmoid region of *Hypophthalmus* is considered to be a derived condition. Other derived states of the ethmoid are those where the bone is flattened with divergent anterior forks (Ageniosidae) is curved ventrally (some Ariidae) or is cavitous with a medially grooved surface (some Auchenipteridae). Another derived form occurs in one group of Pimeloididae, *Piramutana, Hemisorubim, Luciopimelodus, Brachyplatystoma, Pseudoplatystoma* and *Sorubimichthys*. Here the mesethmoid is greatly depressed and

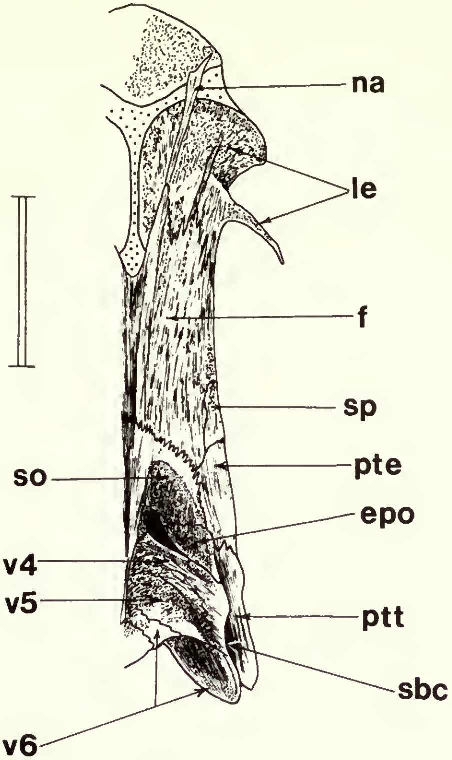

Fig. 16 *Hypophthalmus edentatus*, dorsal view of cranium. Specimen BMNH 1972.7.27: 675–678 (alizarin). Scale = 10 mm.

expanded laterally (Fig. 15). As in *Hypophthalmus* the lateral portion of the ethmoid forms a large cavity wherein lies the olfactory organ (etch, Fig. 15).

Derived conditions of the lateral ethmoid are those where the bone has a posterior process contacting an anterior process of the frontal (some Ariidae and Pangasiidae) and where the bone is extensive, its antero-lateral portion lamellate, extensively cancellous and vacuolate. This latter condition occurs in Pangasiidae, Amphiliidae, Auchenipteridae and Pimelodidae, but among the latter family only one taxon, *Parapimelodus*, approaches *Hypophthalmus* in the width and shape of its mouth.

The mandibular barbels of pimelodids are particularly well-developed and in some taxa, as in *Hypophthalmus,* they articulate with large cartilaginous plates, e.g. *Sorubim, Pseudoplatystoma, Iheringichthys, Pinirampus, Pimelodus* (part), *Luciopimelodus.* The two former genera differ from *Hypophthalmus*, however, in having the barbel origin remote from the jaw symphysis. Ghiot (1978) described the cartilaginous plates in *Pimelodus* '*clarias*' and commented on the elasticity of the plates and their function of supporting and moving the barbels. In *Pimelodus blochii, Iheringichthys, Pinirampus* and *Luciopimelodus* the barbels lie close to the symphysis, the presumed plesiomorph condition, but the cartilaginous supporting plates have a complex form resembling that in *Hypophthalmus* (Fig. 15). These taxa also share with *Hypophthalmus* the peculiar mandibular sesamoid cartilage which supports the lip fold, and the coronoid extension of the Meckelian cartilage (see p. 18 above).

The cranium (Figs 16–18)

There is little purpose in presenting a detailed description of the cranium, already described by Wright (1885). It is necessary only to comment on those features pertinent to the present discussion.

The neurocranium is moderately broad, transversly convex, becoming high-vaulted in the occipital region, and has a deep supraoccipital crest (Fig. 16). All the cranial bones are of a honeycomb texture with the frontal papyraceous. Nearly all sutures are synchondral, and fatty tissue pervades bone-muscle interspaces.

The otic region

The *prootic* is pierced by two foramina (pro, Fig. 17). The hyomandibular and palatine branches of the VII cranial nerve emerge through the posterior one (fhvii) whilst the oculomotor, trigeminal, abducens and facial nerves emerge through the anterior foramen in the border of the bone (ftf).

In almost all siluroids investigated there is but a single foramen piercing or indenting the prootic. In some ariid taxa the prootic is imperforate and the foramen for the cranial nerves is contained within the pterosphenoid. The absence of a second, posterior, opening in the prootic of most siluroids is due to the peculiarity of the cranial blood vascular system in these fishes. In the majority of teleosts the posterior prootic foramen serves for the passage of the jugular vein (lateral head vein) as well as the hyomandibularis nerve trunk. In siluroids, the jugular lies lateral to the cranial wall and is joined by its various branches in the same aperture as that through which the trigeminal nerve complex passes.

The absence of a complete trigemino-facialis chamber in siluroids has been commented upon by several authors as the following quotations indicate:

Allis (1908:259) referring to *Ictalurus* (=*Amiurus*) notes that, 'The artery (external carotid) does not apparently traverse a trigemino-facialis chamber, for although it would seem as if this chamber must be present in some form, there is no proper indication of but one cranial wall in this region, and that one wall would seem to be the inner wall of the chamber; for both the external carotid and the jugular vein lie external to it.'

De Beer (1937:137) again in referring to *Ictalurus* comments, 'There is no lateral commissure or pila antotica. The side wall of the skull in the orbital region therefore presents a continuous fontanelle—the sphenoid fontanelle—between the hind edge of the preoptic root of the orbital cartilage and the anterior basicapsular commissure. . .'

Bamford (1948:365, 367) referring to *Galeichthys*, 'The normal foramina for the exit of the various parts of V and VII are absent, and the exit of these is limited to the sphenoid fissures.' . . .'There is no trace of a pila lateralis or any similar structure.'

Alexander (1965:95) finds that in siluroids, 'The chondrocranium lacks the lateral commissure. The trigemino-facialis chamber of the adult skull has consequently lost its walls.'

All these authors are agreed that the siluroid condition is one where the trigemino-facialis chamber has been modified and the prefacial commissure suppressed. Bamford (1948) suggested that cartilaginous growth from the anterior edge of the otic capsule had crowded the nerves and vessels into the same foramen as the optic nerve (see below concerning the passage of the optic nerve).

The absence or reduction of an internal carotid artery in certain siluroids has also been the subject of comment by Allis (1908), Goodrich (1930), De Beer (1937) and Bamford (1948). According to Bamford (1948) the internal carotid has all but disappeared, with a consequent modification of the arterial circuitry. As yet, too few siluroids have been examined to ascertain the extent of this specialization.

The optic foramen and the suprasphenoid

In *Hypophthalmus* passage of the optic nerve (II) is through a separate foramen between the pterosphenoid (pts) and the 'suprasphenoid' (see below). In many siluroids there is no separate optic foramen, the optic nerve sharing the same opening as the trigemino-facialis

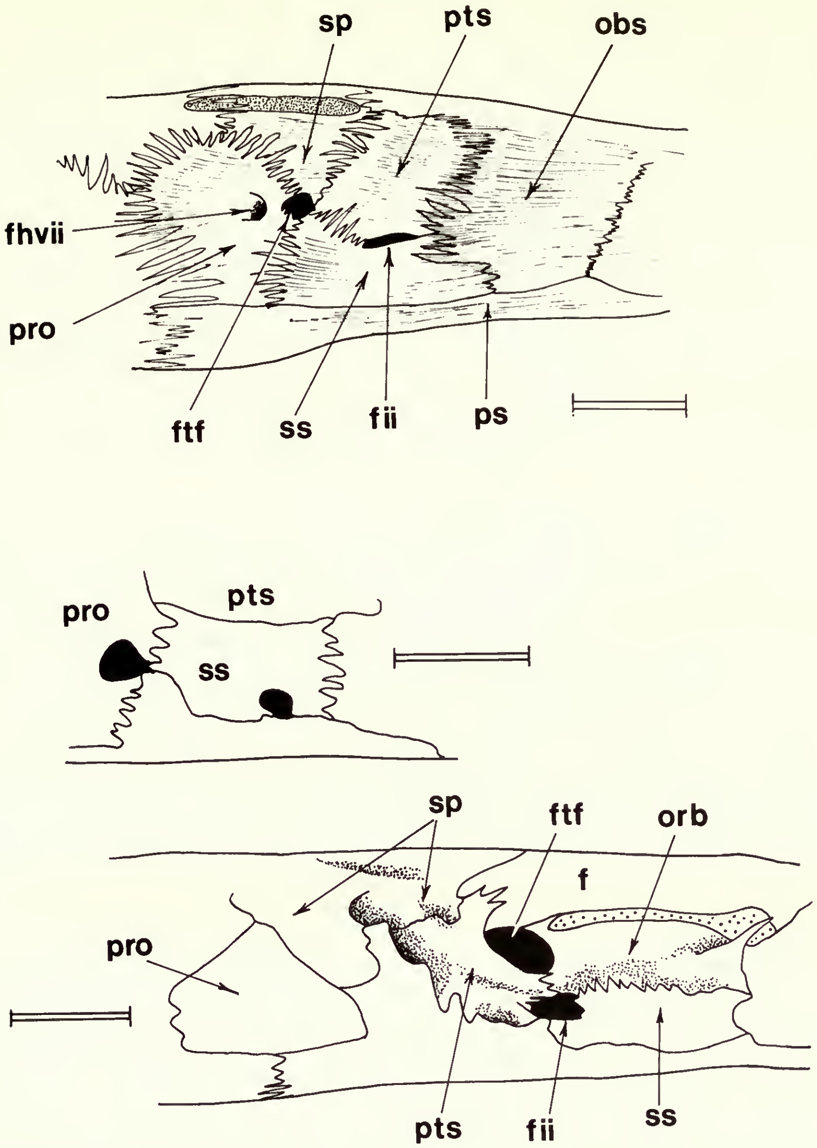

Fig. 17 Neurocranium, otic region of: (upper) *Hypophthalmus edentatus* ventro-lateral view. Specimen BMNH 1972.7.27: 675 (alizarin). Scale = 3 mm. (centre) *Auchenipterus nigripinnis* lateral view. Specimen BMNH 1910.5.26: 12 (skeleton). Scale = 3 mm. (bottom) *Pterodoras granulosus* lateral view. Uncatalogued skeleton. Scale = 10 mm. ss = suprasphenoid.

complex, e.g. Diplomystidae, Callichthyidae, Siluridae, Bagridae (part), Clariidae. It is more usual in siluroids for there to be a separate foramen for the optic nerve between the pterosphenoid and parasphenoid or the suprasphenoid.

Wright (1885) referred to a paired element in *Hypophthalmus* as a basisphenoid. The bone in question is long and shallow and contacts the pterosphenoid, orbitosphenoid and prootic (ss, Fig. 17). Between it and the pterosphenoid is a slit-like foramen through which passes the optic nerve (fii, Fig. 17). In many taxa I have examined a similar element is present, and in the Auchenipteridae and Doradidae it is pierced by the optic foramen (Fig. 17), a feature recognised as synapomorphic.

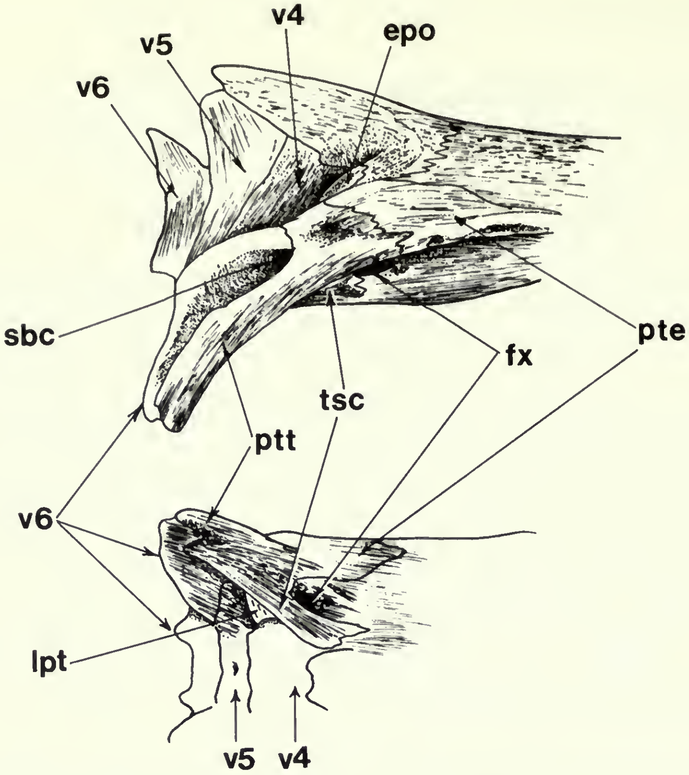

Fig. 18 *Hypophthalmus edentatus* neurocranium, occipital region (upper) in lateral, and (lower) in ventral views. Composite drawing from alizarin and dry preparations. tsc='transcapular'.

McMurrich (1884*a*) and Kindred (1919) have described the so-called basisphenoid in *Ictalurus* (=*Amiurus*). Kindred (1919: 39–40) discussed the homology of this element and decided that the term 'suprasphenoid' rather than basisphenoid would be better applied to it. He defined the suprasphenoid as a '. . .connective tissue ossification above the parasphenoid and between the ventral ends of the alisphenoids (=pterosphenoids).' Daget (1964) also advocates caution in applying the term 'basisphenoid' to this element in siluroids. Thus, Kindred's term, suprasphenoid is adopted here as one being free of any implied homology.

The homology of the siluroid parasphenoid itself is in doubt. Allis (1919) considered the problem in *Ictalurus*, (=*Amiurus*) and argued that the siluroid parasphenoid was an ossification of the ventral myodome roof, the posterior myodome being absent in siluroids.

Bamford (1948:375) remarks that in *Ictalurus*, '. . .there are so many exceptional features in this region of the skull . . . myodome basicranial relations, absence of trigemino-facialis chamber, blood systems, pilae etc—that the matter cannot be regarded as settled.'

Until more is known about the occurrence of the suprasphenoid amongst siluroids, and until more definite information on its ontogeny and relationships with other elements is available, the value of this bone as a taxonomic character cannot be determined.

The occipital region

There are several outstanding features in this region of the cranium in *Hypophthalmus*, not least of which is the ankylosis of the skull and the vertebral column (Fig. 18).

The *supraoccipital* (so) crest is high and posteriorly is firmly united with the succeeding neural spine (4th). Anteriorly the supraoccipital meets the frontal (f), and laterally it is bounded by the epioccipitals. Wright's (1885) description and figure give an incorrect shape to the supraoccipital, and those elements bounding it are misidentified.

Posteriorly the *epioccipital* (epo) is separated from the parapophysis of the 4th vertebrae by an elliptical foramen through which passes the ramus lateralis (Fig. 16). This foramen is shown in Wright's (1885) figures (fe, figs 1 & 3), but in the wrong position, as lying between the pterotic and posttemporal.

The '*posttemporal*' is an extensive bone (ptt, Fig. 18), its anterior part meeting the pterotic (pte) and exoccipital (exo) and its medial margin bordering the parapophyses of the 4th, 5th and 6th vertebrae. In no other siluroid does the posttemporal extend so far posteriorly, nor articulate with the 6th vertebra. The ventral limb of the 'posttemporal' is broad and thick, and articulates with the basioccipital. A thick ligament runs between its upper medial border and the 4th centrum (1pt, Fig. 18).

There has been some considerable debate concerning the identity of the element connecting the cleithrum with the cranium in siluroids. The most recent discussions are by Lundberg (1975) and are reconsidered by Fink & Fink (1981). The latter conclude that the siluroid element is a composite formed from the supracleithrum, possibly the posttemporal and Baudelot's ligament. That part of the element contacting the basioccipital and identified by Fink & Fink (1981) as the ossified Baudelot's ligament was referred to by Kindred (1919) as the transcapular.

I have little to add to this discussion except to confirm Lundberg's (1975) observation that the small plate-like bone (previously thought to be an extrascapular, but identified by Lundberg as the posttemporal) does not occur in the Hypophthalmidae. However, such an element is present in *Luciopimelodus* which I have labelled here as an extrascapular so as to conform with Fink & Fink's nomenclature (es, Fig. 20). Notwithstanding Lundberg's evidence (1975) from the sensory canal pattern that the posttemporal is lacking, it would seem that the supracleithrum would be the element of the clavicular series most 'easily lost' in phylogeny; see for example Rosen (1964) where the supracleithrum is lacking in certain atheriniforms.

The complex vertebrae, swimbladder and posterior lateral line nerve

The complex vertebrae and swimbladder (Figs 19–21)

Both Wright (1885) and Chardon (1968) have described the peculiar nature of the *Weberian apparatus* in *Hypophthalmus*. The most notable character is the complex encapsulation of the swimbladder formed of the parapophyses of the 4th centrum. The parapophyses are produced into dorsal and ventral laminae, the ventral lamina formed partly from superficial ossification; see below p. 28. The cavity so formed provides a capsule housing the swimbladder (sbc, Fig. 18).

Internally the swimbladder (sb, Fig. 19) is divided by a longitudinal septum. Externally it has a thick tunica externa but no tunica interna. The opening between the upper and lower parts of the parapophysis together with the lateral extension of the 'posttemporal' form a funnel-like aperture to the exposed outer wall of the swimbladder (Fig. 19). No transverse duct connects the swimbladder chambers.

The *tripus* (tr) is connected to the tunica externa just anterior to the septum. A medial extension of the tripus articulates with the *complex vertebrae* (3rd centrum). Anteriorly the tripus contacts the *scaphium* (sc) *via* a minute *intercalarium* (ic). The claustrum is lacking. The scaphia provide the walls of the cavum sinus imparis. According to Wright (1885:114), the roof of the cavum sinus imparis is an ossified plate of dura mater attached to the first centrum, but in the preparations examined it seems as if the roof is just a continuation of the exoccipital. The 1st centrum is so far forward that it lies between the exoccipitals and above the basioccipital (v1+2, Fig. 19).

Wright (1885) maintained that the Weberian apparatus in *Hypophthalmus* has been '...pushed (in the process of its reduction) into the foramen magnum, instead of being outside the skull...'. Although that author considered the Weberian apparatus and swimbladder to be functionless (a theory endorsed by Bamford, 1948) this does not appear to be so. The swimbladder is constructed as in other siluroids and there is a mobile articulation of the Weberian ossicles, all of which suggests that the system is functional (see below).

The complex vertebrae and swimbladder in other siluroids

In siluroids, as in other otophysans, the anterior four vertebrae are modified to form the *Weberian apparatus*. However, unlike other otophysans, there is a greater degree of fusion between the centra involved, and the united elements are usually referred to as the *complex vertebrae* (Chardon, 1968). In addition to this fusion of the first four centra, sometimes the 5th, and more rarely the 6th, 7th and even 8th are also incorporated in this complex.

The lateral processes of the various centra incorporated in the complex vertebrae are always well-developed, often forming sheets of bone which may contact one another to provide a dorsal shield to the swimbladder. The anterior ramus of the 4th vertebral parapophysis (following Tavolga, 1962, referred to hereafter as the *Müllerian ramus*) may contact the inferior limb of the 'posttemporal' and, in some taxa where the swimbladder is encapsuled, it may form a substantial part of the capsule. Alternatively, the Müllerian ramus may remain free from the 'posttemporal' and curve ventrally to contact the tunica externa of the swimbladder.

In some families (Doradidae, Auchenipteridae, Mochokidae, Malapteruridae, Pangasiidae, Ariidae) the Müllerian ramus is free from any attachment with the 'posttemporal', its distal tip is expanded into a plate which contacts the tunica externa of the swimbladder. Protractor muscles run from the bony expansion to the cranium and neural spine complex supporting the dorsal fin. Müller (1842) named this mechanism the *Springfederapparat*, now usually referred to as the elastic spring apparatus, and below as the ESA.

The plesiomorph condition of the swimbladder in siluroids is assumed to be one in which

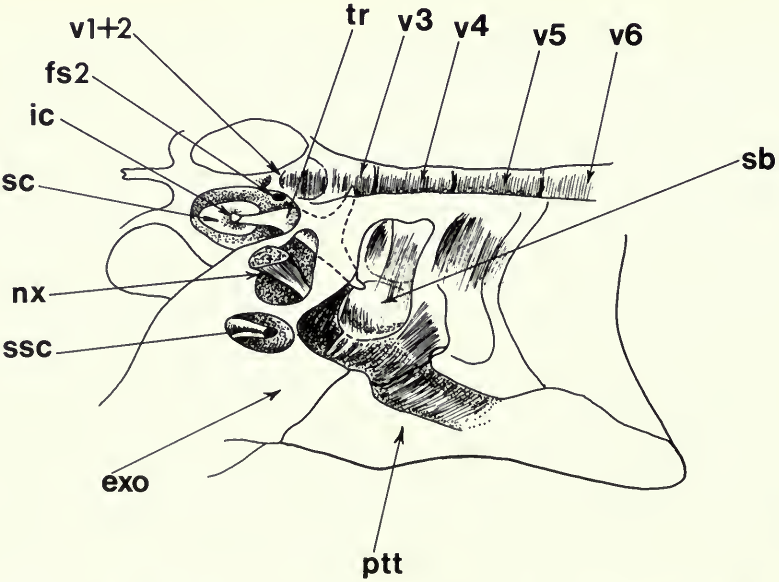

Fig. 19 *Hypophthalmus edentatus* swimbladder and Weberian apparatus. Dorso-lateral view of transverse section through the anterior vertebrae and occipital region. Composite drawing from alizarin and dry preparations. fs2 = foramen of 2nd spinal nerve; ssc = semicircular canal.

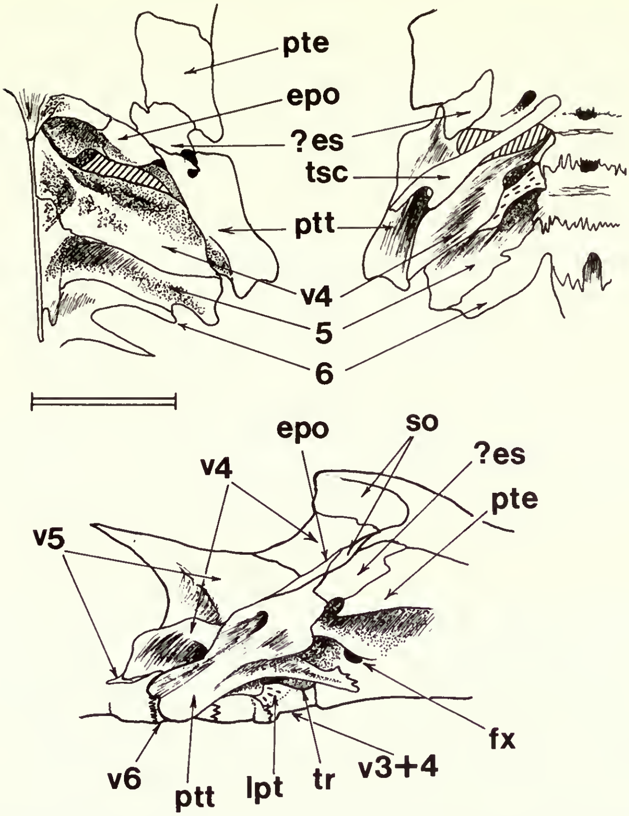

Fig. 20 *Luciopimelodus pati* complex vertebrae in (left) dorsal, (right) ventral, and (bottom) lateral views. Specimen BMNH 1878.5.16: 30, dry skeleton. Scale = 5 mm.

the organ is large and free from any intimate contact with the anterior vertebral parapophyses, the lumen partially divided by a T-shaped septum, and the pneumatic duct entering the anterior transverse chamber. In taxa with this type of swimbladder, the anterior vertebrae (i.e. those following the complex vertebrae) demonstrate a range of fusion patterns, from being completely unfused, Diplomystidae, to the fusion of centra 4–6 in some Pimelodidae. In those taxa with an ESA, the swimbladder is also large and not encapsuled, but it is notable that in all ESA taxa studied the complex centra display the maximal vertebral consolidation (4 – 6 + 4 –7 in some ariids). In those taxa with encapsuled swimbladders, a series of progressive anterior vertebral fusions is apparent. However, only three families have the maximal fusion of 6 centra, Loricariidae, Astroblepidae and Ageneiosidae.

If progressive fusions, namely the 4th centra with the 5th, then fusion with 6th and 7th vertebrae, are taken as successively derived conditions the resulting cladogram indicates that swimbladder encapsulation has occurred independently in at least two lineages (Fig. 22). However, a more rigorous study of the individual taxa within those lineages shows incongruencies in this hypothesised phylogeny. For example, the nature of swimbladder encapsulation in the Callichthyidae, Astroblepidae and Loricariidae is virtually identical, the 'posttemporal' contributing to the lateral wall of the capsule (Alexander, 1964; 1965; Chardon, 1968). These taxa also share a derived rib structure and dermal ossification patterns (see Alexander, 1965). On the basis of vertebral fusion patterns alone, however, these families appear in different lineages. Likewise, the Ageneiosidae also appears with the Loricariidae and Astroblepidae, but the encapsulation of the swimbladder is quite different since it is derived from superficial ossification (see below).

Further incongruencies arise in this phylogeny when the detailed structure of the ESA and the associated swimbladder are taken into account. In the Doradidae and Auchenipteridae the organisation of this system is more elaborate than that of other ESA taxa. In both families the epioccipital has long posterior processes which contact the 5th and 6th parapophyses. Such features are lacking in other ESA groups. From these observations it seems very likely that the ESA has, as in the case of swimbladder encapsulation, been achieved independently in several lineages.

Another incongruency arises if the superficial ventral ossification of the fused vertebral centra is taken into account. Superficial ossifications were described by Bridge & Haddon (1894) as a continuous sheet of bone uniting the paired parapophyses and enclosing the cardinal veins. According to Tilak (1965:170–171) the superficial ossification is derived from the tunica externa of the swimbladder. There is much variability in development of superficial ossification. In some taxa it forms a channel or a complete tunnel enclosing the dorsal aorta. In others it contributes to the anterior part of the swimbladder capsule.

There appears to be a trend for the more derived siluroids to have reduced and encapsuled swimbladders. The most extreme forms of encapsulation and swimbladder reduction are usually encountered among those taxa with accessory respiratory devices, Clariidae, Loricariidae and Callichthyidae. In this respect the Hypophthalmidae and Ageneiosidae are exceptional.

Alexander (1964) makes the point that encapsulation of the swimbladder results '. . .when the anterior parapophyses have not been correspondingly reduced'. Undoubtedly this is so, the anterior (Müllerian) ramus of the 4th parapophysis progressively curving around the swimbladder and meeting the lamina of the 5th appears to be an ontogenetically obvious process of encapsulation. The swimbladder capsule may also incorporate part of the ventral superficial ossification (see above), in Loricariidae and Callichthyidae the posterior cranial bones (epioccipital and 'posttemporal') also contribute to its formation.

Alexander (1964) advanced the hypothesis that a reduced swimbladder volume could have evolved to compensate for increased buoyancy resulting from gas held in the accessory respiratory organ. Qasin & Hasan (1961) suggested that such gas could even be used in buoyancy control. Gee (1976) does not agree, pointing out the unlikelihood of a simultaneous reduction of swimbladder volume (SBV) and development of an accessory air breathing organ (ARO) derived from some other part of the fish's anatomy. Gee also noted that loricariids although possessing the smallest SBV *lack* an ARO. Gee's thesis is that the overiding factor in swimbladder reduction is directed towards a demersal existence wherein a greater variety of environments may be exploited, e.g. substrate burrowing by trichomycterids; leaf litter and bank 'burrowing' by loricariids. Some of these environments, however, tend to be hypoxic and would have demanded compensatory air breathing devices.

Reduction of SBV in Hypophthalmidae and Ageneiosidae is obviously due to different factors than those obtaining in loricariids etc, and ones related to attaining neutral, or near neutral buoyancy. Unlike Old World 'pelagic' siluroids, schilbeids, siluriids and pangasiids, whose neutral buoyancy depends on a large swimbladder, the Hypophthalmidae, and probably the Ageneiosidae, rely on a high body fat content (see p. 5). More positive assertions on the functional utility of SBV reduction can only be made in the light of detailed knowledge of swimbladder physics.

Alexander (1965) states there is no known fish in which the Weberian apparatus is a functionless vestige. However, in loricariids, callichthyids and trichomycterids the ossicles are reduced, the claustrum and intercalarium lacking (see Chardon, 1968). To what degree the absence of these elements impairs or alters the function of the Weberian system is unknown.

Bamford (1948) noted that little work had been done on the ontogeny of the siluroid Weberian apparatus as compared with that in cyprinids. There has been no redress of this situation. Bamford's implication was that the entire Weberian system could have been derived independently in siluroids. This hypothesis has still to be tested.

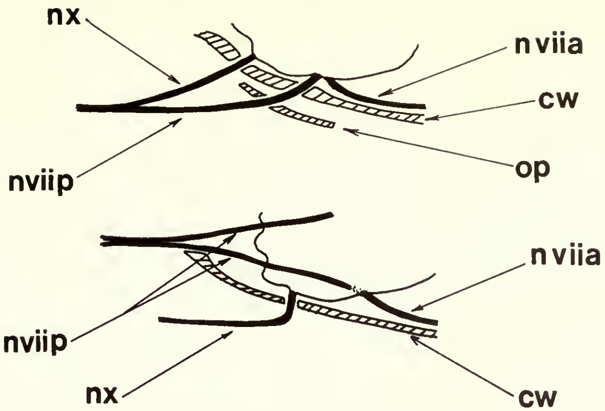

Fig. 21 Pathway of vagus and posterior branch of the facial nerves in gymnotoids (upper), and siluroids (lower). Dorsal view, semi-diagrammatic drawn from dissections of *Eigenmannia virescens* and *Pimelodus blochii*. cw = cranial wall; op = operculum.

The posterior lateral line nerve

The anterior shift and gross re-shaping of the Müllerian ramus in *Hypophthalmus* has necessitated a diversion in the route of the vagal ramus lateralis, posterior lateral line nerve. As a result, after leaving the exoccipital (fX. Fig. 18) it takes an almost vertical course then passes through the foramen between the Müllerian ramus and epioccipital (see above, p. 25), finally, running posteriorly across the dorsal surface of the parapophysis.

Nelson (1960) described the course of the vagus lateralis in *Malapterurus* as leaving the cranium and running laterally along the ossified Baudelot's ligament (inferior posttemporal limb and transcapular of authors) thence passing caudally along the length of the body; the ramus lateralis vagi of authors. Such is the usual course of the nerve in other siluroids investigated. Nelson (1960) also describes a dorsal or recurrent branch of the VII cranial nerve which, after leaving the cranium innervates the dorsal length of the body. This nerve appears to correspond with that described by Mithel (1964) as the ramus lateralis accessorius in *Mystus* and by Juge (1899) as the 'nerf de Weber' in *Silurus*.

The more direct course of the vagus lateralis in *Hypophthalmus* also occurs in *Luciopimelodus* (Fig. 20). Here too the posterior tip of the 'posttemporal' is elongated to extend as far as the 5th parapophysis, and the Müllerian ramus is elevated and strongly curved antero-ventrally to partially encapsulate the swimbladder. These features cause the nerve to follow a vertical route from its exit in the exoccipital and, as in *Hypophthalmus* to pass through a gap between the supraoccipital, epioccipital and Müllerian ramus (Fig. 20).

Nelson (1960) noted that in gymnotoids the '. . .nerve (vagus) emerges from the postero-lateral aspects of the cranium associated with the opercular muscles and passes superficial to the pectoral girdle.'; after which it penetrates the body wall musculature and follows the horizontal myoseptum.

Szabo (1974) following Nelson (1960) considers the *dorsal nerve* in siluroids '. . .to be of the type', presumably homologous, as the *lateral nerve* trunk in gymnotoids. Fink & Fink (1981) accept such a homology as a character in uniting siluroids and gymnotoids as sister groups. The very different pathways of the nerve trunk in these two groups suggests however the possibility of independent derivation.

In siluroids the vagus lateralis passes laterally across the transcapular (tsc) (Baudelot's ligament *fide* Fink & Fink), over the Müllerian ramus and then ventrally, medial to the pectoral girdle. The posterior branch of the anterior lateral nerve (ramus recurvens nervi facialis; ramus dorsalis or ramus lateralis accessorium *auctt*) emerges through the supraoccipital to course along the dorsal aspect of the body (Fig. 21).

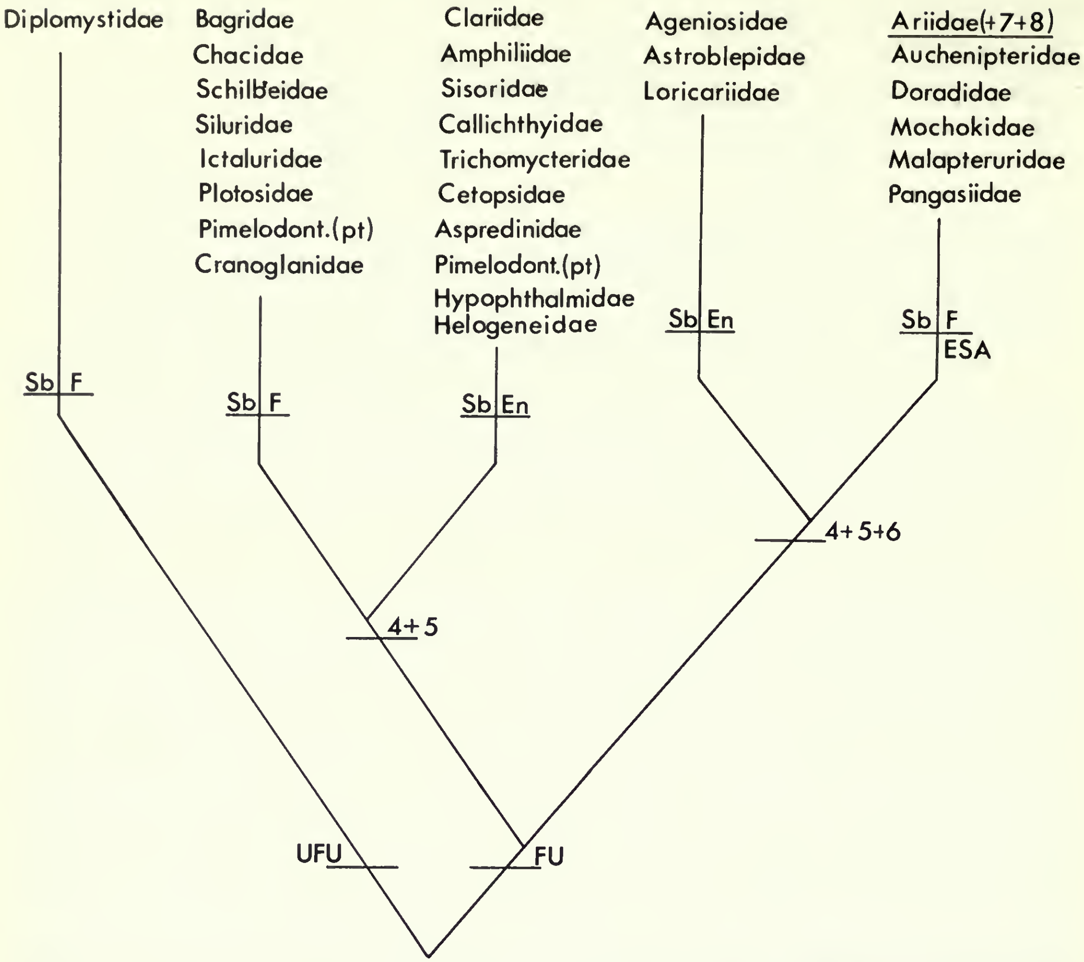
Diplomystidae
Bagridae
Chacidae
Schilbeidae
Siluridae
Ictaluridae
Plotosidae
Pimelodont.(pt)
Cranoglanidae
Clariidae
Amphiliidae
Sisoridae
Callichthyidae
Trichomycteridae
Cetopsidae
Aspredinidae
Pimelodont.(pt)
Hypophthalmidae
Helogeneidae
Ageniosidae
Astroblepidae
Loricariidae
Ariidae(+7+8)
Auchenipteridae
Doradidae
Mochokidae
Malapteruridae
Pangasiidae
Sb F
Sb F
Sb En
Sb En
Sb F
ESA
4+5
4+5+6
UFU
FU

Fig. 22 Cladogram of currently recognised siluroid families based on degree of fusion of the anterior vertebrae and nature of the swimbladder. UFU = vertebrae unfused; FU = vertebrae fused; 4 + 5 + = numbers of centra added to the complex vertebrae; SbF = swimbladder free; Sb En = swimbladder encapsuled; ESA = elastic spring apparatus. For the purposes of the diagram the Clariidae includes the Heteropneustidae. The Pimelodontidae is represented on two lineages, those taxa with an encapsuled swimbladder correspond with group 1 as defined on p. 37. Ariid taxa examined appear to have the 7th (? and 8th) centra added to the complex vertebrae. It is not certain that all ariid taxa have this many consolidated centra. Data mostly from Chardon (1968) and pers. obs.

In gymnotoids the vagus lateralis runs postero-ventrally into the epaxialis and does not pass over the 4th parapophysis. The posterior branch of the anterior lateral nerve does not pass dorsally but laterally, to pierce the hyomandibula, then to run medial to the pectoral girdle, and into the body musculature where it joins the vagus lateralis (Fig. 21).

The suspensorium (Figs 23 & 24)

In *Hypophthalmus* a large pterygoid bone extends between the quadrate and hyomandibula to form a bipartite attachment with the lateral ethmoid. This articulation takes the form of a long triangular portion and an upright process (pty, Fig. 23). Between the two anterior forks a ligament runs anteriorly to attach to a minute bony element and thence to the lateral

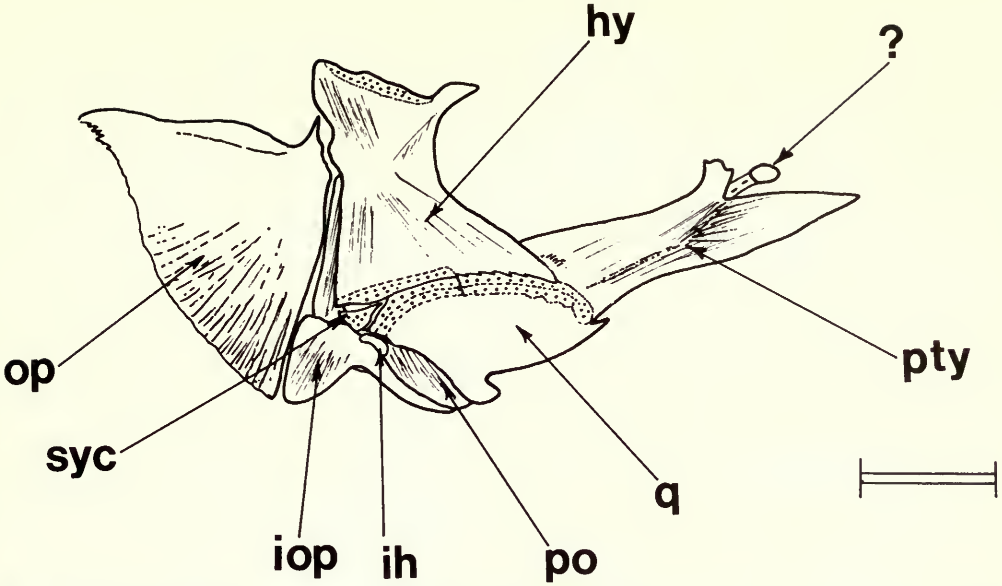

Fig. 23 *Hypophthalmus edentatus* suspensorial and opercular bones, medial view (cartilage dotted). Specimen BMNH 1972.7.27: 675–678. Scale = 5 mm.

ethmoid. The *pterygoid* (pty, Fig. 23) contacts the quadrate synchondrally, and the hyomandibular process *via* a dentate suture. The *hyomandibular process* (hy) extends anteriorly along the dorsal rim of the *quadrate* (q) which it meets synchondrally. The stem shank of the hyomandibula contacts the central dorsal rim of the quadrate *via* a synchondrosis. Posteriorly, it is separated by a wedge of cartilage (syc), which may represent the symplectic. The *interhyal* (ih) articulates between this cartilaginous element, the posterodorsal edge of the quadrate, and the upper rim of the interoperculum.

The identity of the various bones comprising the suspensorium in siluroids is doubtful. Regan (1911) simply referred in pimelodids to 'pterygoids' lying between the hyomandibula and palatine. Compared with most other teleosts the pterygoid series is, for the most part, incomplete since it lacks one of the pterygoid elements usually present. Authors have been at variance as to whether it is the ecto- or endopterygoid which is absent (see comments of Kindred, 1919; Alexander, 1965 and Gosline, 1975).

The problems of identifying siluroid suspensorial elements is illustrated by reference to the pimelodid *Pinirampus* (Fig. 24). The pterygoid is like that of *Hypophthalmus* in having a sharply demarcated ventral portion that articulates with the quadrate, whilst the dorsal portion articulates with the hyomandibular process. An area of cartilage lies between the branches of the pterygoid, the hyomandibular process and the quadrate. Lying close to the anterior border of the pterygoid is a scythe-shaped bone, its elongate portion directed ventrally. The bone is connected to the pterygoid and to the lateral ethmoid *via* ligaments. Between the scythe-like bone and the pterygoid border is a splint-like bone which is attached by connective tissue to both the scythe-like element and the palatine.

Two identification schemes of the suspensorial elements are presented. In one (Fig. 24, left) the pterygoid is considered as the metapterygoid, the scythe-shaped bone as the endopterygoid and the splint-like bone as the ectopterygoid. In the other (Fig. 24, right) the hyomandibula plus metapterygoid are considered as forming a single element, or, alternatively the metapterygoid is considered lost, and the pterygoid as comprising the endo- plus, ectopterygoid. The two isolated bones are problematical. From its position in connective tissue the splinter-like element could be a sesamoid ossification. The scythe-shaped bone is characteristic of one group of pimelodids (see p. 37) and again, may be a

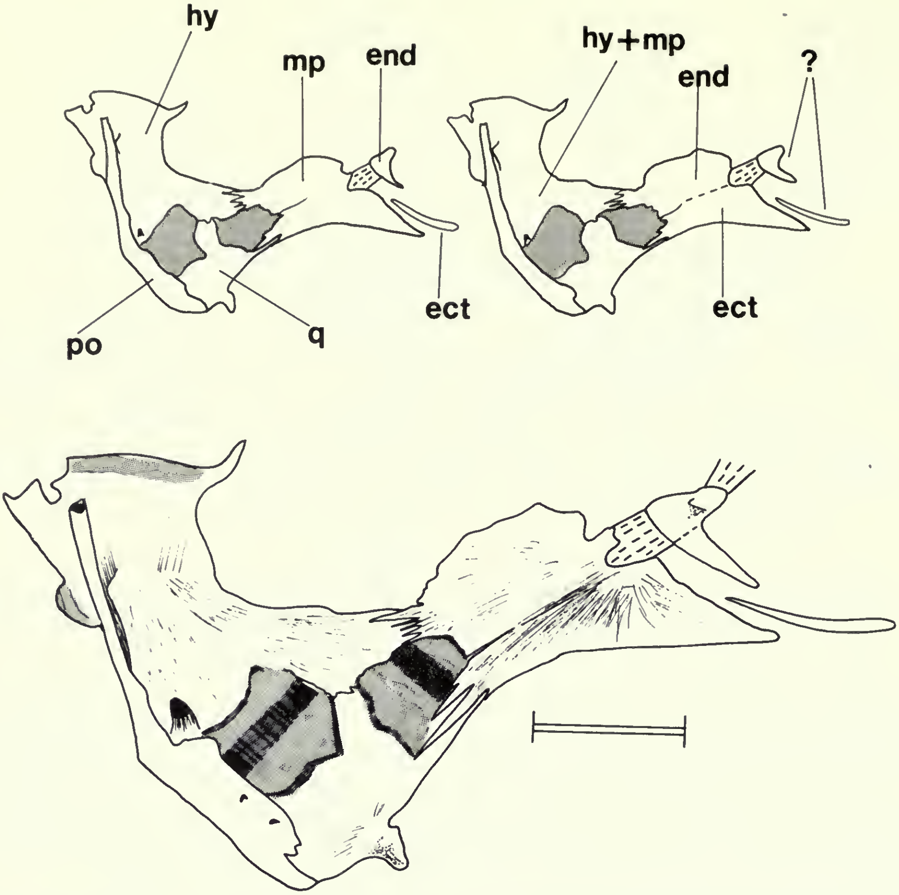

Fig. 24 *Pinirampus pirinampu* suspensorial and opercular (part) bones. Specimen BMNH 1934.8.20: 104–5. Scale = 3 mm. The upper, labelled drawings represent two interpretations of the suspensorial elements. Shaded areas represent cartilage.

sesamoid bone. A small bone occurs in *Hypophthalmus* in a similar position and having the same ligamentous attachments as the scythe-shaped bone in *Pinirampus* (see above). It seems unlikely that these 'isolated' elements represent an ectopterygoid as they occur in the wrong topographical positions. The problem of suspensorial bone homologies in siluroids will be dealt with elsewhere (Banister & Howes, in preparation).

The hyoid arch (Fig. 25)

In *Hypophthalmus* the anterohyal and posterohyal are exceptionally elongate and, unusually, are of equal length. The *anterohyal* (ahy) bears 8 *branchiostegal rays* (bsr) and the *posterohyal* (phy) 6. The *dorsal* and *ventral hyals* (dh, vh) are small and separated from the anterohyal by cartilage. The *interhyal* (ih) articulates with the posterior tip of the posterohyal. The *urohyal* (uh) is a short oval bone lacking a medial ridge.

Gosline (1974) relates the number of branchiostegal rays to the length of the free sleeve of the branchiostegal membrane. This certainly appears to be a valid correlation in *Hypophthalmus* where the gill opening extends very far forward, and may, to a certain extent, be applied to some pimelodid taxa as well. Examples are *Sorubim* and *Pseudoplatystoma* which also possess long gill openings and a high number of branchiostegal rays (11–16).

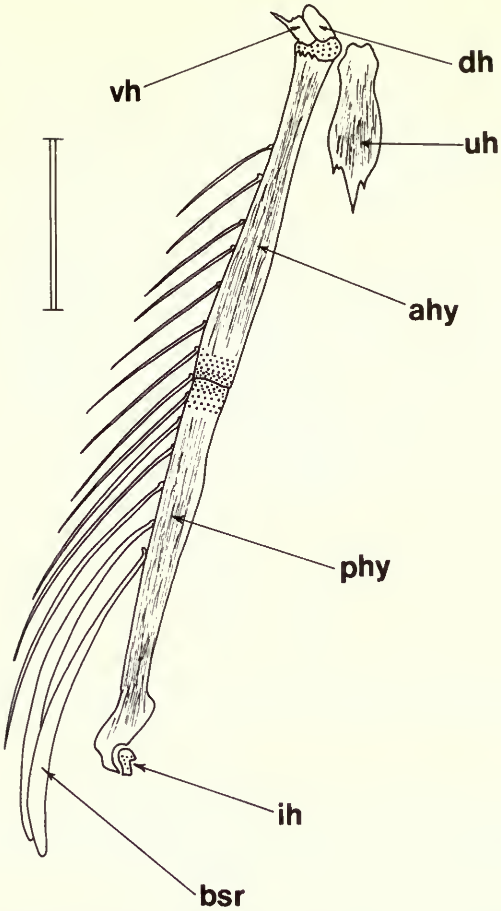

Fig. 25 *Hypophthalmus edentatus* hyoid arch, lateral view. Specimen BMNH 1972.7.27: 675–678. Scale = 5 mm.

According to McAllister (1968) a high number of branchiostegal rays is the primitive condition in teleosts. On this basis he considers that amongst siluroids the Old World taxa '. . .appear to be more primitive than the South American catfishes, having 4–20 branchiostegals as opposed to 3–17. . .'. The extent of these ranges and the degree of overlap hardly justify such a statement. From McAllister's counts for siluroid families, the predominant number of branchiostegal rays would seem to be 9–11 and perhaps this, by virtue of its widespread occurrence, should be thought of as the plesiomorph number rather than the high number advocated by McAllister. Further comparative data, particularly on the morphology and the placement of the branchiostegal rays on the hyoid bar are necessary before any valid statement can be made concerning the apo- or plesiomorphy of their number.

The relationships of the *interhyal* to the preoperculum shows some interesting modifications in the Pimelodidae. The usual siluroid condition, as in other ostariophysans, is for the interhyal to articulate between the quadrate, or symplectic, and the hyomandibular limb. In most siluroids the interhyal attaches, in the absence of a symplectic, ligamentously to both quadrate and hyomandibula, abutting against the intervening cartilage (see description of *Hypophthalmus* above). In *Pseudoplatystoma* the interhyal has shifted posteriorly to such an extent that its connection with the hyomandibula and quadrate is lost,

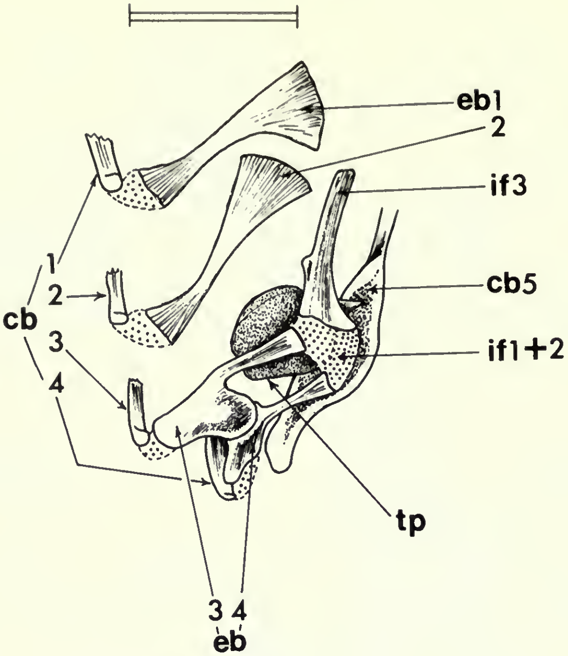

Fig. 26 *Hypophthalmus edentatus* upper and lower (part) branchial arches, dorsal view, left side (cartilage stippled). Specimen BMNH 1972.7.27: 675–678. Scale = 3 mm.

and instead it articulates entirely with a preopercular fossa. Intermediate stages in the development of this condition are to be found in *Goldiella, Sorubim* and *Brachyplatystoma* where the interhyal has shifted even further posteriorly and is ligamentously attached to the rim of a preopercular fossa alongside the hyomandibula.

The opercular series (Fig. 23)

The *preoperculum* (po) of *Hypophthalmus* is a thin, narrow bone covering the posterior margins of the hyomandibula and the quadrate, virtually obscuring the interoperculum. The *interoperculum* (iop) is roughly triangular but with a concave ventral border where it overlaps the pectoral fin base. The *operculum* (op) is almost equilaterally triangular, its posterior edge much fretted, and its entire structure cancellous.

The opercular bones of *Hypophthalmus* appear to be of a 'generalised' siluroid type, i.e. a large operculum, almost vertical preoperculum and small interoperculum. There is considerable variability in size and shape of these elements throughout the Siluroidei (Howes, in press). Fink & Fink (1981) maintain that the triangular shape of the operculum is synapomorphic for the siluroids and gymnotoids. However, whereas the ventro-posterior border of the operculum in siluroids is either straight or concave, that in gymnotoids is more often convex, as in other otophysans.

The gill arches (Figs 26–27)

Upper elements (Fig. 26). The *epibranchials* of *Hypophthalmus edentatus* are narrow-waisted, with expanded medial surfaces and bear 25–27 long, fine gill-rakers, As in all siluroids examined, epibranchial (eb) 3 has an uncinate process which in *Hypophthalmus* is rounded and overlies the central portion of eb4. *Infrapharyngobranchial* (if) 3 is well-ossified and elongate, its posterior margin separated from eb3 and eb4 by a cartilaginous wedge. Of the two alizarin preparations at my disposal, the larger shows two distinct chondrifications in

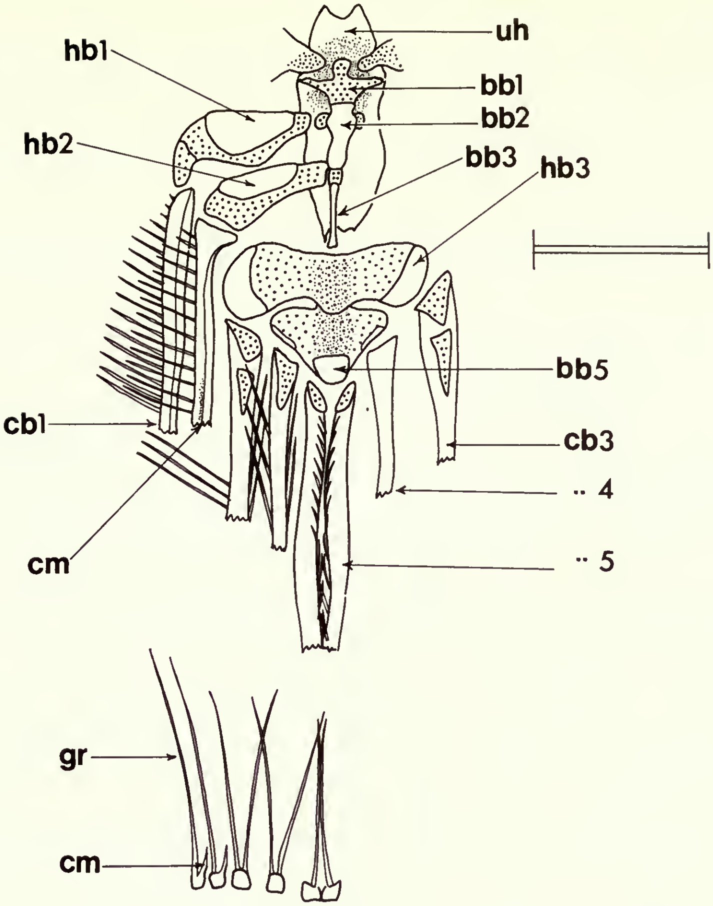

Fig. 27 *Hypophthalmus edentatus* lower branchial arch elements; (upper) dorsal view. Specimen BMNH 1972.7.27: 675–678. Scale = 3 mm; (lower) cross section of left side gill-rakers and ceratobranchials. cm = ceratobranchial membrane.

this wedge. These cartilages suspend a large oval toothplate bearing on its ventral surface many minute, conical teeth (tp, Fig. 26).

Lower elements (Fig. 27). The *basibranchials* (bb) and *hypobranchials* (hb) are poorly ossified. Basibranchial 1 is a triangularly shaped cartilage lying in the plane of the anterohyals; basibranchials 2 and 3 are rod-like ossified elements; basibranchial 4 is incorporated within a broad cartilaginous cornua, the ossified lateral margins of which represent hypobranchials 4; basibranchial 5 is represented by a triangular cartilage whose apex is ossified. Hypobranchials 1–3 are ossified only along their leading edges.

The *ceratobranchials* are the most elongate of any siluroid and carry at least 200 long gill-rakers. The first two ceratobranchials (cb) have only a single row of gill-rakers (gr), along the outer edge; the inner edge has a low wall of fibrous connective tissue (cm). The other ceratobranchials have a double row of gill-rakers; the 5th is dentigerous, its anterior stem is excessively elongate and meets its fellow along the midline. The gill-rakers on cb 5 occur only along the inner margin; anteriorly the rakers of each ceratobranchial intermesh.

Roberts (1972) described the sieving mechanism of the gill-rakers. The arrangement of this mechanism is shown in Fig. 27 as a transverse section of the lower gill-arch. Such an arrangement does not occur in any other siluroid.

Postcranial elements

As this study is concerned primarily with the cranial anatomy of *Hypophthalmus*, no detailed description of the postcranial anatomy is presented. The following features, however, are worthy of note.

The *pectoral girdle* is of simple construction, with a greatly elongated horizontal cleithral limb and the coracoid reduced to a horizontal lamina. Such elongation of the cleithrum is unknown in any other siluroid.

There are 62 *vertebrae*, excluding the complex vertebrae. This is an exceptionally high number amongst siluroids and is exceeded only by members of the Clariidae. Virtually no comparative data exist for vertebral numbers in siluroids. A superficial survey indicates that the mean siluroid count is 40–45. High counts are found among Ariidae 49–50, Ageneiosidae 49–50, Siluridae 50–51 and Clariidae 60+. Among the Pimelodidae only *Luciopimelodus* has an exceptionally high count 47–48.

The *caudal fin skeleton* of *Hypophthalmus* is of a plesiomorph pattern with no fusion of any hypural elements (PH;1;2;3;4;5). Lundberg & Baskin (1969) found hypural fusion and reduction of principal caudal fin rays to be widespread conditions. The most derived hypural fusion patterns occur in the Plotosidae, Chacidae and Loricariidae. In the latter family there is also an expansion of the last neural spine, which contacts the upper caudal element, *i.e.* the fused hypurals 3–5, uroneural and epural. Certainly the derived caudal fusion patterns shared by the Loricariidae, Callichthyidae and Astroblepidae are congruent with synapomorphies involving the encapsulation of the swimbladder (see p. 27).

Other caudal fin patterns are not so easy to interpret and characters such as the absence of an hypurapophysis in the Clariidae and Plotosidae are interpreted as parallelisms by Lundberg & Baskin. Although both clariids and plotosiids trend toward anguilliform morphology, it is interesting to note that the hypural fusion pattern in clariids (excluding the Heteropneustidae) is, in contrast to plotosiids, plesiomorph. Even in such a seemingly derived taxon as *Allabenchelys* all the hypurals are free.

Amongst the Pimelodidae, the predominant caudal fusion pattern is a free parhypural; 1+2; 3+4; 5, which as Lundberg & Baskin (1969: 40) remark is significantly more advanced than that of any bagrid. The hypural fusion patterns yield little support for the proposed groupings of pimelodids presented below, except that *Rhamdia* and *Pimelodella* share a similar fusion of hypurals, 1+2 and 3+4.

Relationships of the Hypophthalmidae

Anatomically, the Hypophthalmidae is a unique group. No other siluroid has such an arrangement of the eye musculature, hypertrophy of the jaw adductor muscles, reduction of ethmoidal ossification, complexly developed mandibular barbel supporting elements, elongated gill- and hyoid arch elements, and profoundly modified vertebral and swimbladder elements.

Attention was drawn in the Introduction to the poverty of published data on siluroid comparative anatomy. In order to apply cladistic methods in resolving interrelationships extensive comparisons must be made thus, at this stage one cannot, with any degree of certainty identify plesiomorph or apomorph characters amongst siluroids. However, from this survey it is clear that the sister-group to the Hypophthalmidae lies within the Pimelodidae. Synapomorphies are manifest in the structure of the ethmoid region, the mandibular barbel articulation, the eye muscle arrangement, the complex vertebrae, and the sensory canal system. The following is a synopsis of these characters:

1. Ethmoid region with lateral cavity (p. 20)—shared with *Luciopimelodus, Pinirampus* and *Pimelodus* (part).
2. Articulation of the mandibular barbels with large cartilaginous plates (p. 21)—shared with *Luciopimelodus, Iheringichthys, Sorubim, Pinirampus, Pseudoplatystoma, Pimelodus* (part).

3. Anterior eye musculature of tendinous origin—shared with *Sorubimichthys*
4. Network of epidermal canals crossing the orbital and opercular regions—shared with *Luciopimelodus* and *Iheringichthys.*
5. Posterior extension of the 'posttemporal' passing beyond the edge of the Müllerian ramus, elevation of that ramus, and vertical path of the anterior portion of the vaugus lateralis nerve—shared with *Luciopimelodus.*

In the course of this study only a limited number of pimelodid taxa was studied, but even this preliminary investigation reveals that there are at least three major groups contained within the Pimelodidae as presently recognised, *viz*:

1. Those species with the swimbladder partially encapsuled and usually with a caecal posterior border; the 5th and 6th fused within the vertebral complex; the ventral superficial ossification of the 4th and 5th centra forming a tunnel for the dorsal aorta; absence of a *retractor tentaculi* muscle.

Included taxa: *Iheringichthys, Pinirampus, Callophysus, Parapimelodus, Pimelodina, Perugia, Megalonema, Luciopimelodus, Pimelodus* (part). In addition, the first four genera and *Pimelodus maculatus* all have a scythe-shaped pterygoid bone lying anterior to the main pterygoid series and attaching to the lateral ethmoid via a ligament (p. 31).

2. Those species with the swimbladder well-developed, not encapsuled, and with attached muscles (see below); 6 vertebrae forming the anterior complex centrum, the 4th and 5th centra elongate and forming an aortic tunnel. A *retractor tentaculi* muscle present.

Included taxa: *Pseudoplatystoma, Sorubim, Hemisorubim, Pimelodus* (part).

The distribution of swimbladder muscles throughout the Pimelodidae as a whole has still to be recorded. Bridge & Haddon (1894) described swimbladder compressor muscles in *Pseudoplatystoma*, (their *Platystoma*) as originating from the occiput and inserting on the antero-ventral wall of the swimbladder. These authors also described a *tensor tripodis* muscle in *Pseudoplatystoma* and some other pimelodontid taxa. This muscle runs from the exoccipital and inserts tendinously into the anterior wall of the swimbladder.

Alexander (1965: 110) was unable to trace the *tensor tripodis* in *Pimelodus blochii*, Alexander's *P. clarias*. However, it appears in this species as a mere strip of tendinous fibres. The muscle is also present in *Sorubim* and *Hemisorubim*

3. Those species with the swimbladder well-developed, not encapsuled, and without compressor muscles; 5 fused centra, sometimes with superficial ossification but without an aortic tunnel. The lateral ethmoid is transversly convex.

Included taxa: *Rhamdia, Pimelodella, Heptapterus*

The above groups include taxa presently distributed amongst four subfamilies, the Pimelodinae, Luciopimelodinae, Callophysinae and Sorubiminae. None of the three groups defined here corresponds with any subfamily as presently recognised. In addition, there is another subfamily, the Pseudopimelodinae (Gomes, 1946). Representatives of this latter group have not been thoroughly investigated in the course of this study, but in those that have been examined the anterior part, at least, of the swimbladder is divided by an extension of the complex vertebrae.

No meaningful phylogenetic classification is accomplished in recognising the above named pimelodid subfamilies, based as they are on a mixture of plesio- and apomorphies. Similarly, placing the Hypophthalmidae in a separate suborder (Chardon, 1968) simply to recognise its morphological distinctiveness, serves no purpose in elucidating its relationships.

From the characters analysed above synapomorphies have been identified that indicate the sister group of the Hypophthalmidae to be in that assemblage which includes *Luciopimelodus* and *Iheringichthys.* A more refined definition of this group must await a thorough anatomical study of the Pimelodidae.

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A revision of the genus *Epiclintes* (Ciliophora: Hypotrichida) including a redescription of *Epiclintes felis* comb. n.

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Introduction

Several hundred species of ciliated protozoa have now been documented from marine interstitial sediments (Dragesco, 1974). However few of these organisms have been adequately described; indeed some forms although regularly encountered in the extensive literature on this group (Hartwig, 1980) have never been redescribed since the original accounts given by Muller (1786) and Ehrenberg (1830). In an early study, Fauré-Fremiet (1950) put forward the hypothesis that interstitial ciliates had a cosmopolitan distribution. This has subsequently been proved correct (Hartwig, 1977), and it has been recognised that these organisms may play a dominant role in the benthic ecosystem (Fenchel, 1969). The opportunity to redescribe one such truly cosmopolitan species came with the discovery of large numbers of the highly contractile hypotrich ciliate *Epiclintes felis* (Muller, 1786) comb. n. in muddy creeks near the estuary of the river Thames. A brief glance through the literature concerning this species indicated that it had been poorly described. In addition there was some confusion concerning synonymies and it was apparent that a revision of the genus *Epiclintes* was long overdue.

Materials and methods

Epiclintes felis were collected from two locations on the south shore of the Thames estuary: Oare creek, National Grid reference TR0163 and Faversham creek, National Grid reference TR0262. Both locations are near Faversham, north Kent. The organisms were found in small shallow (5–10 cm) lagoons just below the high tide line along the sides of the two creeks. They were found on the surface of the fine mud and detritus at the bottom of the lagoons or beneath the surface film of the water. The salinity of the water was 70% sea water (SW). Subsequently this species has been found at two sites on the north shore of the Thames, at Shoeburyness, Essex, National Grid reference TQ9485. At this locality the organisms were found firstly at the sand surface, 20 metres from shore, and secondly in association with the red alga *Ceramium* sp. collected 10 metres from shore. All sites were permanently covered with water at low tide.

Cells were cultured in filtered 70% SW, pH 7·8 at 18°C under constant illumination from an 8 W fluorescent lamp. Subcultures were made every 5 days. Some difficulty in handling the organisms was experienced due to their thigmotactic nature and inate fragility but when quickly transferred using a wide bore micropipette, this problem was solved. Silver stains of the cortex were prepared by the method of Tuffrau (1967). Silver stained preparations were supplemented by observations using Nomarski interference, phase contrast and brightfield

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illumination, photographs and video recordings. It was found that good structural preservation could be obtained with certain fixatives, consequently some specimens were prepared for transmission electron microscopy. Two methods of fixation were employed:

(1) Nouzarède's Method (Nouzarède, 1977) for fragile ciliates. The specimens were first fixed in 2% osmium tetroxide in 70% SW neutralised with solid calcium carbonate, for 10 minutes. They were then rinsed in 70% SW and transferred to 10 drops of sea water to a dish and two drops of 25% glutaraldehyde (also neutralised with solid calcium carbonate) were added. The organisms were fixed in this solution for 30 minutes. The ciliates were then returned to the osmium solution for a further 20 minutes.

(2) Specimens were fixed in a solution of equal parts of 3% glutaraldehyde in phosphate buffer and 1% osmium tetroxide in phosphate buffer for 20 minutes. These two fixatives were prepared in Millonig's buffer (Millonig, 1961).

In both cases the ciliates were washed in 10% ethanol and then dehydrated in graded alcohol solutions before being embedded in TAAB resin. Sections were stained in a saturated solution of uranyl acetate in 50% ethanol for 10 minutes, followed by 0·4% lead citrate in 0·1 M NaOH (CO_3^{2-} free) for 5 minutes. The first fixative preserved the pellicle most effectively and the second was employed to preserve the subpellicular structures.

Nomenclature

Epiclintes felis (Muller, 1786) was first identified by Muller (1786) under the name *Trichoda felis.* Although the description was terse and the accompanying diagram gave little information, it is still possible to recognise this very distinctive hypotrich. Muller (1786) described the form of the body as being slightly curved and transparent. It was rather rotund but posteriorly attenuated in the 'tail'. The ventral surface was seen to be covered by 'vibrating hairs' which covered the surface of the 'trunk' right up to the apex of the tail. Bory St Vincent (1824) added a little more information to Muller's description and transferred the organism to the genus *Oxitricha* as *O. felis.* He noted that the tail was frequently held curved. Once again the diagram of the species gave few details as to the placement of the cirri. The organism was also independently decribed by Claparède & Lachmann (1858) as a new species in the family Oxytrichina, *Oxytricha auricularis.* Without knowledge of Muller's *T. felis,* these authors gave a fairly detailed account of their 'new' species. They carefully described the characteristic shape of the body and the fact that the dorsal surface was seen to be ornamented by 'short batonnets' implanted in the tegument. Detailed information regarding arrangement of cirri was lacking.

In his paper of 1862, Stein proposed the name *Epiclintes auricularis* to combine Muller's (1786) *T. felis* and *O. auricularis* of Claparède & Lachmann (1858). Stein (1864) gave the first detailed description of *E. auricularis* and supplied further details in his major work (Stein, 1867). However Stein (1862) was in error in attributing the specific name '*auricularis*' to his new genus *Epiclintes.* Since the name '*felis*' was presented in 1786, 70 years before *O. auricularis* was published, the earlier name must take precedence. The correct name of the taxon is *Epiclintes felis* (Muller, 1786) comb. n. Diesing (1866) was the third author to independently identify *E. felis* and ascribe it to a new genus; *Claparedia* Diesing, 1866. Although an invalid name, his useful description noted that the peristome of the organism was situated asymmetrically and the body was extremely plastic or deformable. It was also noted that the tail region was highly contractile and caudal 'styli' were seen to be present.

Wallengren (1900) in his description of the organism he called *Epiclintes ambiguua* made a taxonomic error which has subsequently led to great confusion. He stated that the species *E. ambiguua* was first named by Stein (1862) after Muller's (1786) original description of *Trichoda ambiguua.* This is incorrect, Stein (1862) described *E. auricularis,* based on the description of *T. felis* Muller (1786). However Muller (1786) did describe a *T. ambiguua* but it is doubtful if this organism is a hypotrich and most certainly does not belong in the genus

Epiclintes. Kahl (1932) failed to note the error and adopted the name *E. ambiguus*; so that subsequently the name *E. ambiguus* appears regularly in the literature. Apart from this lapse in the nomenclature of the organism, Wallengren (1900) went on to give an excellent description of his species, which was undoubtedly *E. felis.* Since these first accounts, many workers on interstitial ciliates have included information regarding this hypotrich, but none has clarified the important details of cirral arrangement, division and behaviour.

Morphological Description

Epiclintes felis (Muller, 1786) comb. n.

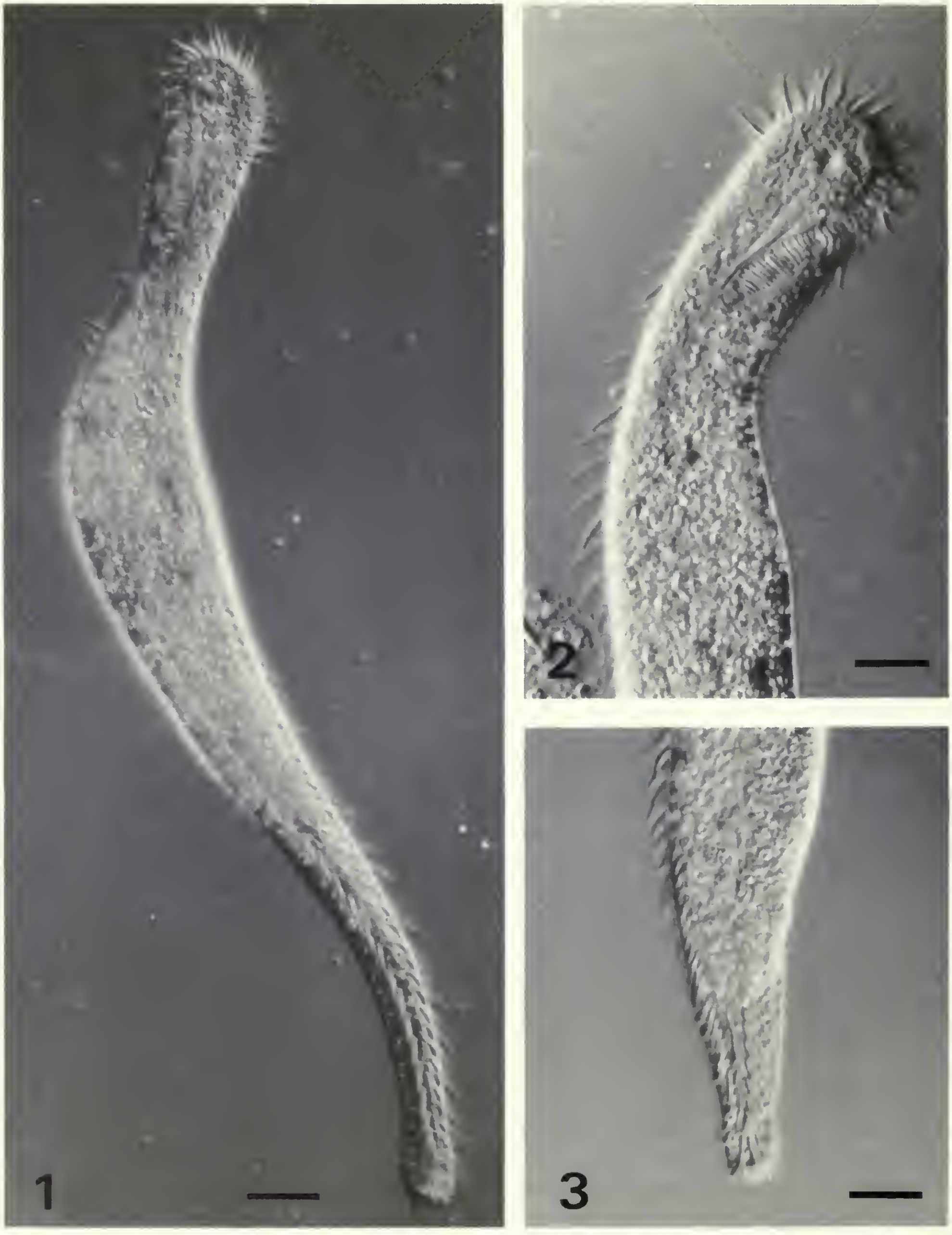
E. felis may be described as a genuinely psammophilic species, that is to say, it can be found on, or at least temporarily associated with, sand of the intertidal zone rather than between the interstices. From Figs 1 & 4 it can be seen that the body of this hypotrich is divided into three distinct regions; a dorsoventrally flattened 'head' region leading via a thin neck to a rotund 'trunk' which terminates in an attenuated 'tail'. Many authors have commented on the fact that the organism is highly contractile, with the ability to shorten to at least 25% of its initial length. It is quite clear that the diversity of form recorded for this species is the result of the organism having undergone contraction to a varying degree. All observations recorded here are based on extended cells unless otherwise stated. However in either contracted or relaxed state, the three regions of the body are a permanent feature. The true appearance of the body is best seen when the organisms have been left undisturbed for some time. In normal locomotion over the substrate, the body is held extended and frequently slightly curved. The head and tail regions are transparent but the central trunk region is translucent and is frequently seen to be full of food materials. In culture *E. felis* was seen to feed on bacteria but frequently, in freshly collected material, diatom frustules were seen within the body. The hypotrich is colourless but Bütschli (1887–1889) noted a yellowish tint. Claparède & Lachmann (1858) were the first authors to quote an accurate size for *Oxytricha auricularis.* They recorded a length of 300 μm. Other reports quote a range of sizes varying from 200–300 μm, Stein (1864, 1867), Mereschkowsky (1879), Rees (1884), Kahl (1932). In this study the species was found to vary in size between 100–350 μm.

'Head' Region

This region illustrated in Figs 2 & 5 is anteriorly rounded and dorsoventrally flattened. It is truly auriform or 'ear-like' hence the etymology of Claparède & Lachmann (1858). In extended, normally moving animals, the head is equal to or one and a half times as broad as the trunk region. Many earlier authors regarded the trunk as possessing greatest breadth but it is clear that their observations were based on at least partially contracted animals. From Fig. 5 the asymmetric adoral zone of membranelles (AZM) extends around the anterior head region on the ventral surface and along the left side of the oral area entering a distinctive tubular buccal cavity. The cytopharynx is clearly visible but the cytostome is not. The AZM itself comprises some 25–35 fine membranelles held erect. These are twice the length of the cirri on the body, and extend as far as the buccal oveture. Here the membranelles form a distinctive 'cage'.

'Trunk' Region

This region is ovoid tapering anteriorly to the head region and posteriorly to the elongated tail. Its length varies with the degree of contraction; in the extended state it is at least twice the length of the anterior portion. When contracted it may equal the head region in length. In normal locomotion the surface of the cell adjacent to the substrate is somewhat flattened. This would account for the thigmotactic nature of this region. On contraction the dorsal surface of the organism becomes distinctly convex in shape, the ventral surface retaining its flattened appearance. This central region may become distended by food material. The contractile vacuole is single and as Kent (1880–1882) has correctly stated, it may be situated centrally or may be found on the left near the termination of the peristome field. The cytoproct is clearly visible at the dorsal surface, just at the junction of the trunk region and tail. The number and form of the macronuclei has been poorly described; early authors described this organelle as a single hoop-shaped body. The macronuclei are in fact small



Figs. 1–3 *Epiclintes felis* photographed by Nomarski interference microscopy: (1) Entire organism, dorso-lateral view, bar represents 10 µm; (2) 'Head' region, ventral view, bar represents 7 µm; (3) 'Tail' region, ventral view, partly contracted, bar represents 8 µm.

and numerous and are, as Wallengren (1900) noted, spherical or ovoid. Due to difficulties in staining this hypotrich, the micronuclei have never been observed.

'Tail' Region

The tail is relatively long, see Figs 1 & 4, at least the length of head and trunk combined, and tapers quickly from the hind regions of the trunk, then less so to its end which is gently rounded. As seen from Figs 1 & 3 this caudal region is very characteristic due to the arrangement of cirri which give it a plaited or braided appearance, especially when contracted. Kahl (1932), for example, noted that it resembled a fishbone. It is usually dorsoventrally flattened and distinctly ribbon-like. This region is highly contractile, much more so than the head or trunk. Possibly longitudinal contractile fibres, akin to the myonemes of peritrich ciliates, are present in the tail as shortening is so rapid. These could contribute to the braided appearance seen so clearly on contraction. The tail serves to periodically jerk the body backwards during normal locomotion. Also on shortening it is frequently noticed that the tail may bend or flex at the junction with the trunk region. It has the ability to bend at least 90° from the longitudinal axis of the cell without sustaining damage. Many of the early workers noted correctly that this region contained no food materials.

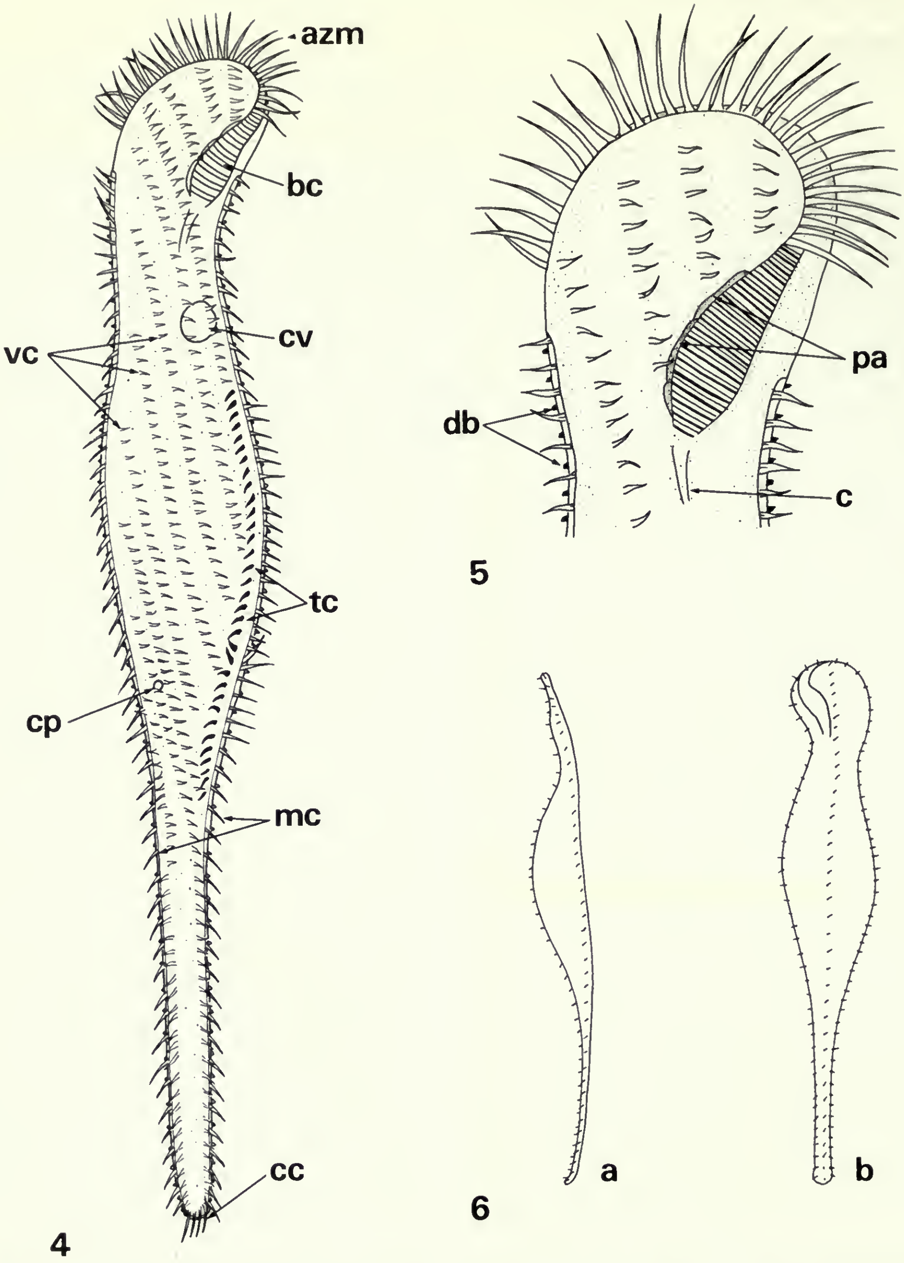
Cirri

Dorsal Cirri

It can be seen from Fig. 6 that the dorsal surface of the organism is ornamented by sensory bristles, which take the form of very short non-motile cilia each apparently arising from a shallow pit. There are three distinct longitudinal rows of single, equally spaced bristles in *E. felis.* The first row arises at the edge of the peristome at the extreme anterior edge of the cell, passes over the head in the midline thence to the trunk and terminates at the posterior extremity of the tail. This row is most easily observed from the lateral view. The two other rows lie on the dorsal surface, at the lateral edges of the organism. They pass round the anterior margin, down the sides of the body and meet the first row at the extremity of the tail. Claparède & Lachmann (1858) were the first authors to identify these organelles in this species. These were the 'batonnets of the tegument'.

Ventral Cirri

Unlike the dorsal surface, the ventral surface of *E. felis* is equipped with many rows of short cirri. These take the form of thick bristles that taper distally. They are used extensively in swimming. Bütschli (1887–1889) noted correctly that these cirri constantly oscillate. Due to the constant movement of the organism and the translucency of the trunk region, it was very difficult to observe the numbers and arrangement of cirri without silver impregnation methods, and this could account for the great discrepancies reported by earlier workers. The ventral surface of the head region is equipped with three diagonal rows of cirri, Fig. 5, running right to left from the extreme right margin of the cell to just over two thirds the width of the body. The first lies parallel to the long axis of the cell, the second and third becoming rather more diagonal. The third row terminates at the end of the buccal cavity. Again, almost impossible to observe without staining is the paroral apparatus which runs from the base of the buccal cavity and part way up its right side. The membranes are small and may be subdivided into two or three parts. The fourth ventral row, which may be termed the first row of the trunk region, starts in the head, passes close to the end of the buccal cavity but continues over the trunk region becoming less diagonally slanted as it does so. The cirri in these rows are fairly short and stumpy and are all separated to the same degree, thus cannot be sub-divided into frontoventrals or midventrals. Stein (1864, 1867) and Bütschli (1887–1889) both stated that three rows were present in this area. Again the number of rows of cirri on the trunk region has been poorly reported. Earlier authors did not state clearly whether or not these ventral rows extended into the tail. Muller's (1786) description gave four or five rows for this central portion while Stein (1864, 1867) claimed six or seven.



Figs. 4–6 *Epiclintes felis:* (4) Entire organism, ventral view, (azm) adoral zone of membranelles, (bc) buccal cavity, (cv) contractile vacuole, (tc) transverse cirri, (mc) marginal cirri, (cc) caudal cirri, (vc) ventral cirri, (cp) cytoproct; (5) 'Head' region, ventral view, (db) dorsal bristles, (pa) paroral apparatus, (c) cytopharynx; (6) Lateral **a**, and dorsal **b**, views illustrating arrangement of dorsal sensory bristles.

Claparède & Lachmann (1858) noted five short strong rows in the tail region but these probably included rows of marginal cirri which are known to be present, no definite number of trunk rows is mentioned in their description. Rees (1884) claimed a total of twelve rows over the entire body, his diagram shows eight on the trunk and one on the tail. Mereschkowsky (1879) gave a total of twenty for the entire cell, nine for the central portion and five upon the tail. The excellent diagram of Perejaslawzewa (1886) shows a total of seven, three on the anterior and four on the trunk, two of which continue into the tail. Wallengren's (1900) description of *E. ambiguua* depicted six oblique ventral rows on the trunk and six rows beginning in the mid-trunk region and entering the tail. Nevertheless it can be seen that there are eight rows running diagonally across the body from right to left (Figs, 4 & 7), the last two enter the tail region and are continued to the tip, passing near the mid-line. These cirri are of similar length and are equally separated, but all of the eight rows can only be visualised in stained preparations. Frequently it is seen that these rows of cirri become interlaced and form a distinctive crest down the mid-line of the tail.

Marginal cirri are a characteristic feature of this hypotrich species, see Figs 1 & 4. There is a continuous peripheral row of short marginals beginning just behind the termination of the peristome field on both right and left sides, which pass down the lateral edges of the body and join at the apex of the tail. The cirri on the right side appear slightly longer than the left. Stein (1864) noted bristle-like marginals whilst Calkins (1902) showed that they projected from the lateral edges and that they were elongated at the posterior of the cell. The two marginal rows lying at the periphery of the tail and the two ventral rows lying adjacent to the mid-line have, in earlier reports, often been seen as four separate rows in this caudal prolongation. A band of transverse cirri, clearly distinguishable from the ventral cirri by their separate rhythm of oscillation, run down the left side from the first trunk row to the first beginnings of the tail (Fig. 7). They approximate in size and shape to other cirri of the ventral surface. A very short band of caudal cirri, numbering four or five emerge from the ventral surface of the tail. These are finer and slightly longer than the ventrals and marginals and are the caudal 'styli' seen by earlier workers.

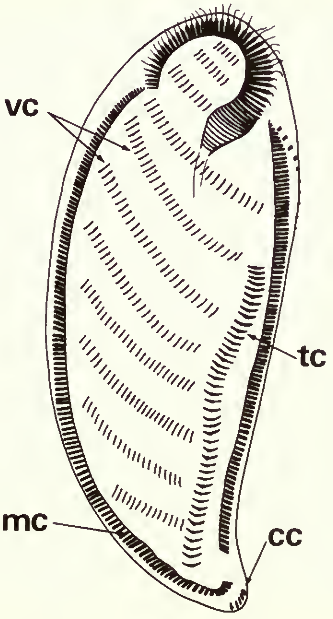


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Fig. 7 *Epiclintes felis*, ventral view of silver stained preparation, (tc) transverse cirri, (mc) marginal cirri, (cc) caudal cirri, (vc) ventral cirri.

Division

Division in *E. felis* was observed on a few occasions during this study but precise details are lacking, therefore a description of stomatogenesis and associated development is not given. Wicklow (1979; pers. comm.) clarified the events accompanying stomatogenesis in this unusual hypotrich. In a detailed study of its morphogenesis he found that *E. felis* possessed a ventral primordium from which many of its ventral rows develop. The row of transverse cirri develop from the posteriormost ends of proter and opisthe cirral streaks. Fission is isotomic, the opisthe retaining the elongate tail and the proter swimming away from division with a simple cylindrical body. The new AZM was seen to develop from the anteriormost of the transverse cirri, in the mid-trunk region.

Ultrastructure

When sectioned, *E. felis* is seen to be unique with the dorsal surface of the cell covered by a multilamellate pellicle of about sixteen layers thick (Fig. 8). This thick pellicle extends down either side of the organism but is modified on the ventral surface. In the vicinity of the ventral cirri the pellicle reverts to the more normal ciliate structure (Pitelka, 1969), but in other regions the multilamellate appearance is seen but the number of layers is reduced to five or six. This unusual pellicle does not extend up onto the dorsal sensory bristles but terminates in a funnel-shaped structure (Fig. 9) rather than a simple pit as seen for example in *Euplotes* (Ruffolo, 1976), which surrounds the base of the organelle. The repeat distance in this thick pellicle is about 6 nm, thus giving a total width for the pellicle of about 100 nm. The lamellae have the appearance of a series of unit membranes in a collapsed condition. The existence of this multilayered pellicle and its function in this highly contractile hypotrich is certainly worthy of further investigation.

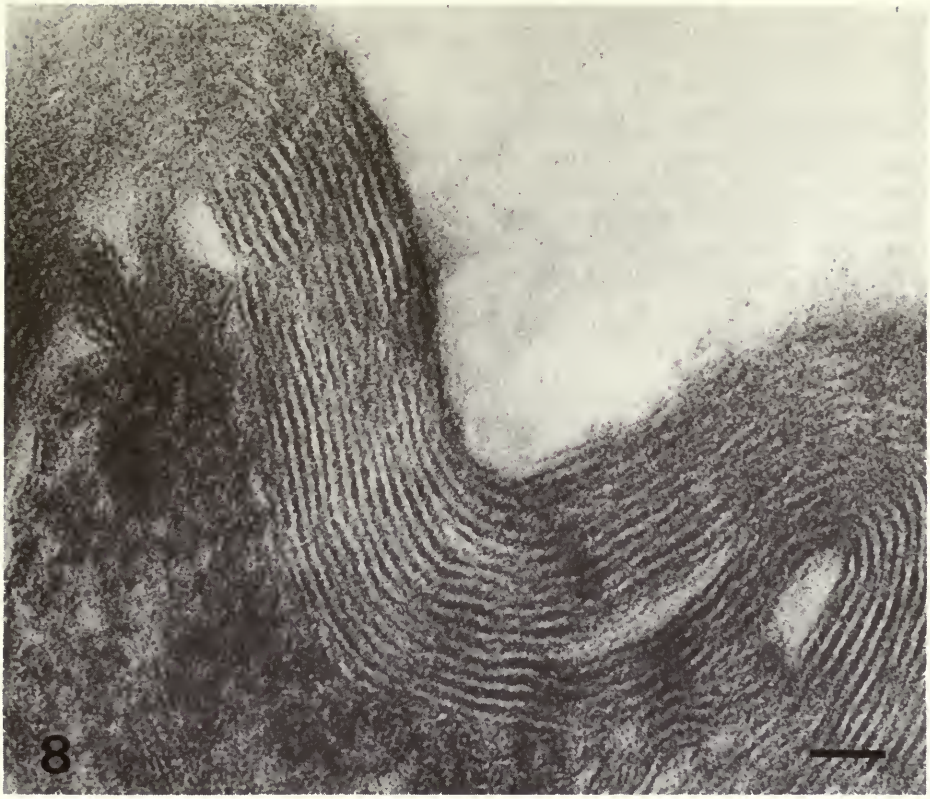
Diagnosis of the Genus *EPICLINTES* Stein, 1862

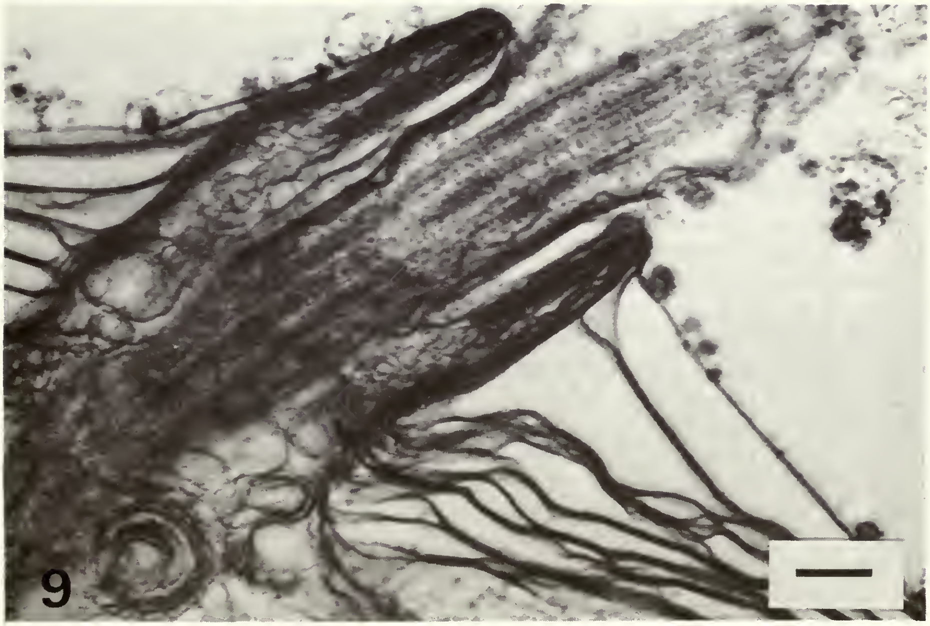
Trichoda Muller, 1786 (In part)
Oxytricha Claparède & Lachmann, 1858 (In part)
Claparedia Diesing, 1866

A free swimming genus of hypotrich, with a flexible and elastic body. The organism exhibits characteristic cycles of contraction and relaxation. The body is divided into three regions; anteriorly the head is dorsoventrally flattened, bounded at the apex of the cell by the peristome. It tapers gradually to the central portion which is cylindrical. The trunk is twice the length of the head and is usually filled with food materials and granular inclusions. The posterior portion takes the form of an attenuate tail, the length of which may roughly equal or extend to at least three times the length of both head and trunk combined. The trunk and tail are flattened ventrally contributing to the organisms thigmotactic abilities. The peristome is asymmetric, commencing right and enlarging as it traverses the anterior of the cell. The AZM terminates on the left, within the head region, in a distinct buccal cavity. Paroral membranes are present on the right side of this buccal cavity. The ventral surface of this organism is equipped with several rows of short stumpy cirri passing longitudinally or diagonally across the body. These cannot be separated into frontoventrals or midventrals. Marginal cirri are placed in one or two rows along the sides of the trunk and tail. A row of transverse cirri is present, running from just behind the peristome to where the trunk narrows at the start of the tail. A short band of caudal cirri is present also at the tip of this tail. Marine.

Species Descriptions

From the literature, nine species have been attributed to the genus *Epiclintes* Stein, 1862. Clearly some of these species are not valid and some have been described on more than one





Figs. 8–9 (8) Electron micrograph of *Epiclintes felis* illustrating the multilamellate pellicle of the dorsal surface, fixed by method 1. The pellicle is 16 layers thick with a repeat distance of 6·2 nm, bar represents 40 nm; (9) Electron micrograph of *Epiclintes felis* illustrating a section through a dorsal sensory bristle, fixed by method 2, bar represents 0·1 µm.

occasion. Thus study reduces the number of nominal species to three, *E. felis, E. caudatus* Bullington, 1940 and *E. radiosa* Calkins, 1902. Corliss (1979) noted that one species of *Epiclintes* resembled the genus *Uncinata*. However no member of the genus *Epiclintes* recorded in the literature resembles this giant species with its characteristic beak-like uncinus.

Two species that have been assigned to the genus, but differ fundamentally from the others are *Epiclintes vermis* Gruber, 1884 and *Epiclintes pluvialis* Smith, 1900. *E. vermis* with its vermiform body closely resembles other hypotrich genera such as *Holosticha*. *E. pluvialis* superficially resembles *Epiclintes* but clearly is in possession of a symmetrical peristome. It lacks ventral cirri and the dorsal cirri were said to be long and 'hispid'. These two species differ sufficiently from the diagnosis of the genus *Epiclintes* to warrant exclusion.

Key to species of *Epiclintes*

1	Frontal 'styles' absent	2
–	Frontal 'styles' well developed, numbering four or five	***radiosa***
2	Ventral cirri in two longitudinal rows	***caudatus***
—	Ventral cirri in eleven diagonal rows	***felis***

Epiclintes felis (Muller, 1786) comb. n.

Trichoda felis Muller, 1786
Oxitricha felis Bory St Vincent, 1824
Oxytricha auricularis Claparède & Lachmann, 1858
Epiclintes auricularis Stein, 1862
Epiclintes ambiguua Wallengren, 1900
Epiclintes ambiguus Kahl, 1932

DIAGNOSIS A psammophilic species commonly found on or adjacent to the sand surface. The body is characterised by its extreme flexibility and contractility. When extended, three regions of the body are apparent. There is a typically auriform anterior, a cylindrical 'trunk' region and an elongate 'tail'. The peristome is asymmetric running around the apex of the cell and into a buccal cavity on the left. The paroral apparatus is small and is situated on the right of the buccal cavity. The cytopharynx is clearly visible. The width of the anterior is equal to, or one and a half times as broad as the trunk. This central region tapers posteriorly to the tail. It is translucent and full of food materials. The contractile vacuole is single and placed centrally or just behind the peristome. A cytoproct lies adjacent to the dorsal surface at the junction of trunk and tail. Macronuclei are small, oval and numerous. The tail is elongate, at least the length of the anterior and central portions combined. It is rounded at the tip and often displays a plaited appearance. The dorsal surface is equipped with three longitudinal rows of sensory bristles, running from the extreme anterior to the tip of the tail, one in the mid-line, the other two at the lateral edges. Ventrally the head is equipped with three rows of short cirri running diagonally from right to left. The trunk has eight rows similarly arranged, the last two of which enter and run down the tail. These two progress right to the tip. Two lateral rows of marginal cirri are present, beginning near the peristome and extending to the point of the tail. A longitudinal row of transverse cirri runs down the left side of the trunk, beginning at the first trunk row and terminating where the tail region begins. In addition, a short row of four or five caudal cirri are present at the extremity of the tail. A prepared slide of *Epiclintes felis* stained by the silver impregnation technique of Tuffrau (1967) has been deposited in the collection of the British Museum (Natural History), accession number 1982 : 2 : 12. Average length 100–300 μm but may shorten to at least 25% of this initial length. *Epiclintes felis* has been recorded from many locations. Claparède &

Lachmann (1858) found the organism on the coast of Norway and noted that it had also been collected in the Baltic Sea. Stein (1864) similarly found this species in the Baltic but more recent researches have shown it to be truly cosmopolitan. Hartwig (1977) gave an extensive list of its distribution and locations will only be listed briefly here; North Sea, Baltic Sea, White Sea, Gulf of Naples, French Adriatic and Mediterranean Coasts, Black Sea, Caspian Sea, Sea of Japan, Bay of Bengal, American Atlantic Coast, Coast of Mauretania, Brazilian Coast and the Coast of Great Britain.

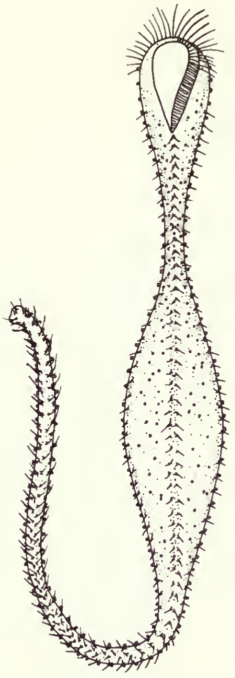


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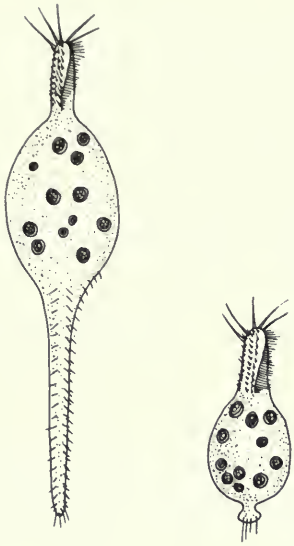
Fig. 10 *Epiclintes caudatus* After Bullington, 1940, ventral view.

Epiclintes caudatus Bullington, 1940

Diagnosis (Fig. 10) A very long and slender hypotrich, widest centrally and dorsoventrally flattened. It is extremely extensile and contractile. The body is divided into three regions, the anterior portion is almost but not quite equal to the central portion in width. The 'tail' is long and narrow, slightly enlarged at the tip. The peristome is asymmetric and traverses around the head region terminating in a buccal cavity on the left side. Sensory bristles emerge from the dorsal surface, at the lateral edges of the cell, beginning in the mid-peristome region and extending to the tip of the tail. Two longitudinal rows of ventral cirri are present, situated on either side of the midline. Two rows of marginal cirri are also present. In the original description the colour was said to be yellowish and the length at rest was 354 μm and the width 28·6 μm. The three regions of the body, an asymmetric AZM, the presence of dorsal sensory bristles, marginal cirri and a high degree of contractility contribute to the inclusion of this species in the genus *Epiclintes.* Only two rows of ventral cirri were noted, running longitudinally. This, together with a very elongate head region and a very long tail process serve to distinguish it from *E. felis.* A marine species isolated from the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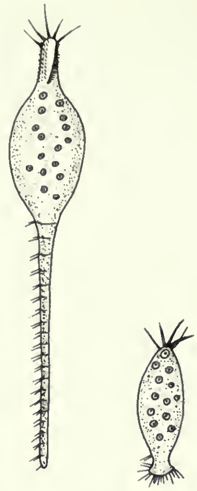
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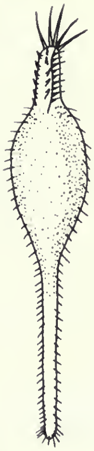
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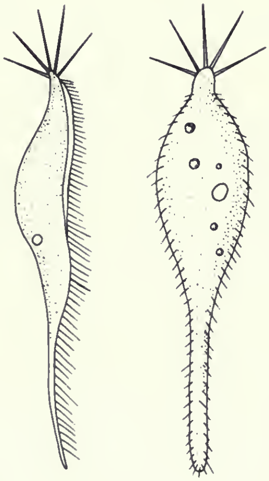
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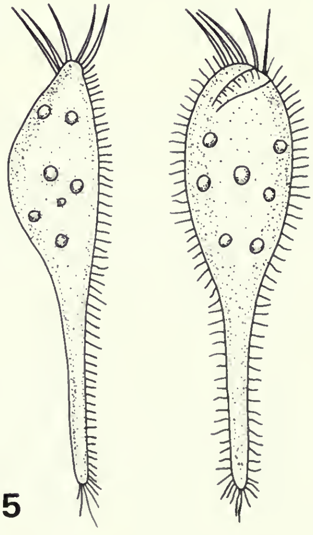
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Figs. 11–15 (11) *Oxytricha retractilis* After Clapareide & Lachmann, 1858, ventral view of relaxed and contracted organisms; (12) *Oxytricha longicaudata* After Strethill-Wright, 1862, ventral view of relaxed and contracted organisms; (13) *Mitra radiosa* After Quennerstedt, 1867, lateral and ventral views of relaxed organism; (14) *Mitra retractilis* After Kahl, 1932, ventral view of relaxed organism; (15) *Epiclintes radiosa* After Calkins, 1902, lateral and ventral views of relaxed organism.

West Indies. These organisms usually swim in left spirals but when locomoting over a substrate or the underside of the surface film they were seen to move without spiralling, in circles, to the left and right.

Epiclintes radiosa Calkins, 1902

Oxytricha retractilis Claparède & Lachmann, 1858
Oxytricha longicaudata Strethill-Wright, 1862
Mitra radiosa Quennerstedt, 1867
Epiclintes retractilis Kent, 1881–1882
Mitra rectractilis Kahl, 1932

DIAGNOSIS A marine species which like *E. felis* has been described by many authors in various states of contraction. *O. retractilis* Claparède & Lachmann (1858) and *O. longicaudata* Strethill-Wright (1862) were both described in the extended state. (Figs 11 & 12). They identified three distinct regions of the body, a narrow anterior with asymmetric peristome, a central region that was distinctly ovoid and an elongate highly contractile 'tail' which nearly disappeared on shortening. Strethill-Wright (1862) noted that this tail had a plaited appearance. Five long anterior cirri were observed by both authors. Quennerstedt (1867), Kahl (1932) and Calkins (1902) all described the organism in the contracted state whereupon the tail shortens considerably and the head and central portions tend to be seen as a single unit. Quennerstedt (1867) (Fig. 13) noted the organism was five times as long as broad and that five long straight frontal cirri, he termed 'styles', were present. This author also noted that a single row of marginals were present upon each side of the anterior and central portions, and a double row bordered the tail. Kahl (1932) noted that *M. retractilis* had a short row of five transverse cirri by which the organism attaches to the substrate. Again four or five long frontal bristles were noted (Fig. 14). Calkins (1902) described the peristome as wide on the right and narrowing as it approached the left side of the body, mention was also made of attachment to the substrate by posterior cirri (transverse cirri) of the tail (Fig. 15). Kahl (1932) was the first to group these independently described organisms under the name *Mitra retractilis.* However as Kent (1881–1882) had already pointed out, the name *Mitra* had previously been assigned to a genus of mollusc and was therefore preoccupied. Thus Kahl's designation is invalid. The additional description by Calkins (1902) erected the name *Epiclintes radiosa* for the organism described by Quennerstedt (1867). The sizes quoted for these organisms are 80 µm for *O. retractilis,* 75 µm for *M. retractilis* and 45 µm for *E. retractilis.* This marine species has been recorded from Norway, Scotland, Heligoland, Kiel Sea, Finland, White Sea and the Atlantic Coast of the USA. Vital information on numbers and arrangement of cirri are unfortunately lacking, but they have been grouped due to the characteristic frontal cirri and the conspicuous highly contractile tail. Further information is required on this interesting species before a definite decision can be taken regarding its validity.

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Notes on the Family Lekythoporidae (Bryozoa, Cheilostomata)

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Introduction

(*a*) *Cheilostome Ovicells*

In recent years, several kinds of cheilostome ovicell have been investigated, and the origins and relationships of the various body wall layers involved have been traced through ontogeny. As a result, it has become obvious that the ovicell, which may be regarded as all the walls defining and protecting the brood chamber and the contained embryo, has several very different origins. Ovicells may be derived wholly, or in part, from diverticula of terminal walls or from extensions of frontal walls and, or, frontal shields. They may be derived wholly, or in part, from one or more zooids. They may be modified, interzooidal, frontally budded kenozooids, or may be formed from one or more kenozooids budded from the maternal zooid, which produces the ovum, or from a sequentially distal zooid or zooids (see Cook, 1979 for brief review). The general term 'ovicell' may therefore be defined functionally, but not morphologically, and it appears that the protective coverings for brood chambers have often been evolved convergently and show only superficial similarities.

All ovicells which have been investigated in detail, and all those which may be inferred by inspection to have analogous ontogeny, are 'distal' in position to the opening edge of the operculum of the maternal zooid. Generally, this 'distal' orientation is also the same as the direction of budding of zooids 'away from' the ancestrula as the colony develops. Even in colonies with 'reversed frontal budding' (where the distal part of the orifice is directed towards the ancestrular region, see below), the opening of the ovicell is placed close to the orifice of the maternal zooid, on that side of the operculum which opens to allow protrusion of the lophophore (see Cook & Lagaaij, 1976). This position is correlated with the position of the coelomopore through which the ovum passes to the exterior. In all cheilostomes which have been investigated, the coelomopore is placed at the base of the 'distal' pair of tentacles. Passage of ova into ovicells is achieved by protrusion of the lophophore and apposition of the coelomopore to the ovicell orifice (see Silén, 1945).

Proximally placed ovisacs, which are principally uncalcified have been reported in the anascan genus *Aetea*, but their ontogeny may be intussusceptive and quite unlike that of other known ovicells (Cook, 1977). Proximal calcified ovicells have also been described in several cheilostome ascophoran genera, which were grouped together in the family Lekythoporidae by Levinsen (1909), and further reviewed by Canu & Bassler (1929). The reported occurrence of 'proximal' ovicells infers that the position of the coelomopore, or at least the behaviour of the maternal lophophore, is radically different from all other cheilostomes in only one group, the Lekythoporidae. Such a difference would be fundamental, although it could be postulated for the genus *Inversiula* (Microporellidae), which is apparently equally aberrant, and where the operculum is hinged distally (see

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Moyano, 1972). The brood sac in *Inversiula* is an interior diverticulum of part of the cuticular outer body wall (tentacle sheath) housed in specially enlarged brooding zooids. The operculum is orientated almost vertically, which would apparently allow passage of ova from a partially protruded lophophore into the ovisac in the 'normal' manner. This has never been observed in living specimens, but Nielsen (1981) has described passage of ova into ovicells closed by the operculum, in which the lophophore was not protruded, but was dimorphic, with very short tentacles.

The hingeing of the operculum in the Lekythoporidae is not like that of *Inversiula* and investigation of specimens of the five genera attributed to the family shows that the ovicell is placed in the 'normal' distal position with respect to the orifice, but that the pattern of astogeny is one of 'reversed frontal budding'. The modifications in zooidal morphology resulting from this type of growth are described below.

(*b*) *Frontal budding and colonial and zooidal morphology*

Frontal budding is a common phenomenon only in cryptocystidean ascophorans, although it occurs sporadically, in a modified form, initiating overgrowths in umbonuloid ascophorans and some anascans. In some cryptocystidean ascophorans, columns of successive, frontally budded zooids may occur (see Banta, 1972, fig. 1 (1), 3). Each zooidal element arises as an intussusceptive expansion of frontal cuticle, with underlying epidermis, of the primary zooid of the series. These together form the boundary wall of an expansion of hypostegal coelom, which is presumed to be provided with nutrients from the visceral coelom by means of the marginal frontal septulae in the frontal calcified shield. As the cuticle-covered bud reaches its full size, a secondary cryptocystidean frontal shield, also with marginal septulae, grows into, and partitions, its coelom into visceral and hypostegal elements. Cryptocystidean frontal shields are interior walls (see Boardman & Cheetham, 1973), and because there is communication between hypostegal and visceral coeloms, these zooids have the potential to form successive series of frontally budded members vertically to the horizontal plane of the primary zooids. Functionally, frontally budded zooids may be regarded as being identical to primary zooids budded through septulae in distal or lateral walls; but morphologically, they may also be regarded as extensions only of the originating primary zooid, because they have no basal walls. An even more integrated kind of frontal budding is found where more than one primary zooid contributes to the development of more than one frontal bud. These interzooidal frontal buds may form nodular masses or erect branches, and are sometimes composed of groups of integrated polymorphic zooids with differing functions (e.g. *Hippoporidra*, see Cook, 1983). Frontally budded zooids frequently have morphologies and orientations different from those of the primary series (see Boardman *et al.*, 1969, fig. 5), and apart from not possessing basal walls, often have no recognisable lateral walls.

In some minute, globular colonies, all budding is frontal, and the position and orientation of the zooids is rigidly patterned and 'reversed' with respect to the direction of growth. In these forms, the distal side of the orifice, the side on which the operculum opens, is directed towards, not away from the ancestrular area, as it is in 'normal' colony growth. In addition, all the calcified walls may be regarded as frontal shields, which consist of a 'concealed' portion, from which new frontal buds arise, and an 'exposed' portion which surrounds the orifice (see Cook & Lagaaij, 1976). Combinations of 'normal' and 'reversed' orientations of frontal buds occur in the genus *Sphaeropora* (see Cook & Chimonides, 1981).

In the Lekythoporidae all colonies are known or inferred to have minute, encrusting bases. In *Lekythopora* and *Poecilopora* zooids are budded distally from the ancestrula for only one or two astogenetic generations. The rest of the colony is composed of erect branches of frontally budded zooids, each of which is orientated with the distal edge of the orifice towards the outer face of the branch. Each zooid bud arises interzooidally from more than one zooid of the earlier astogenetic generation and develops a cryptocystidean frontal shield with numerous frontal septulae. Fully formed zooids are vase-shaped or columnar and all the vertical calcified walls (whether axial or peripheral) form one continuous 'frontal' shield.

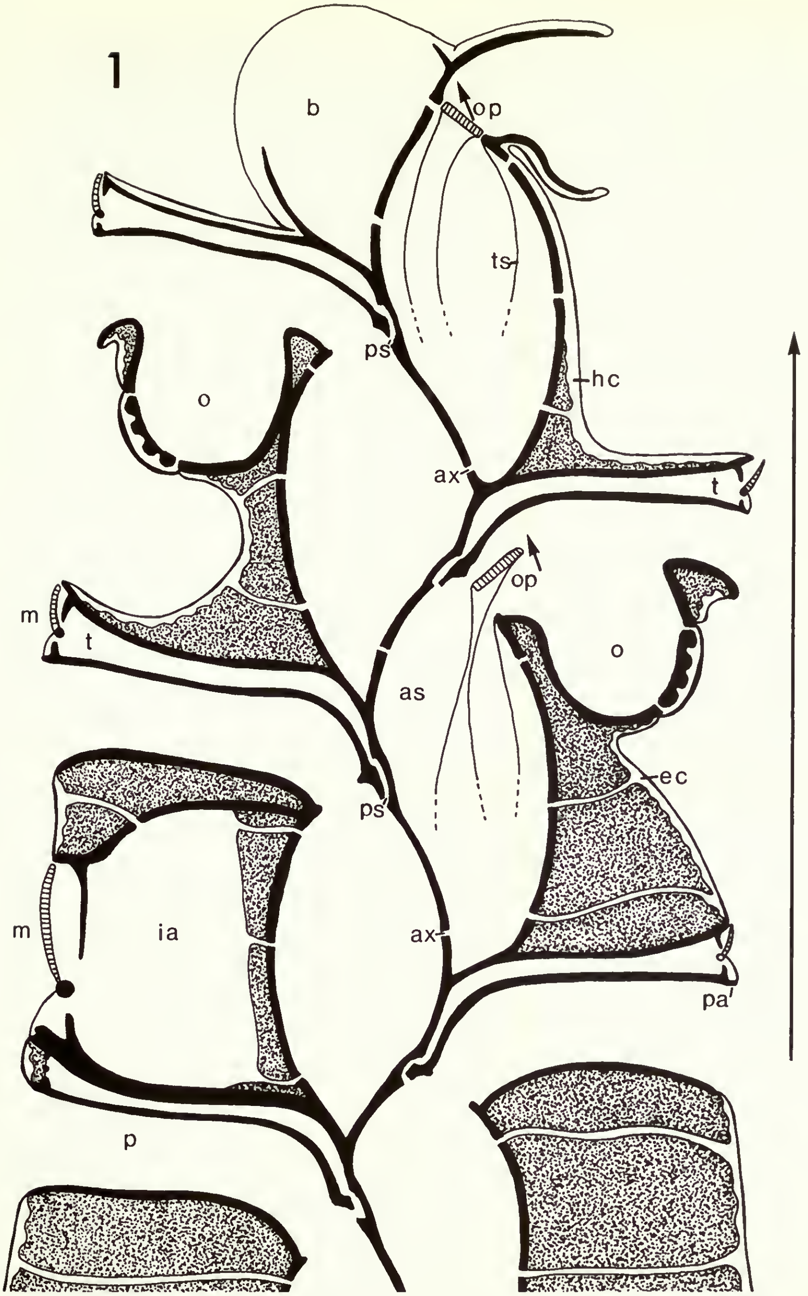
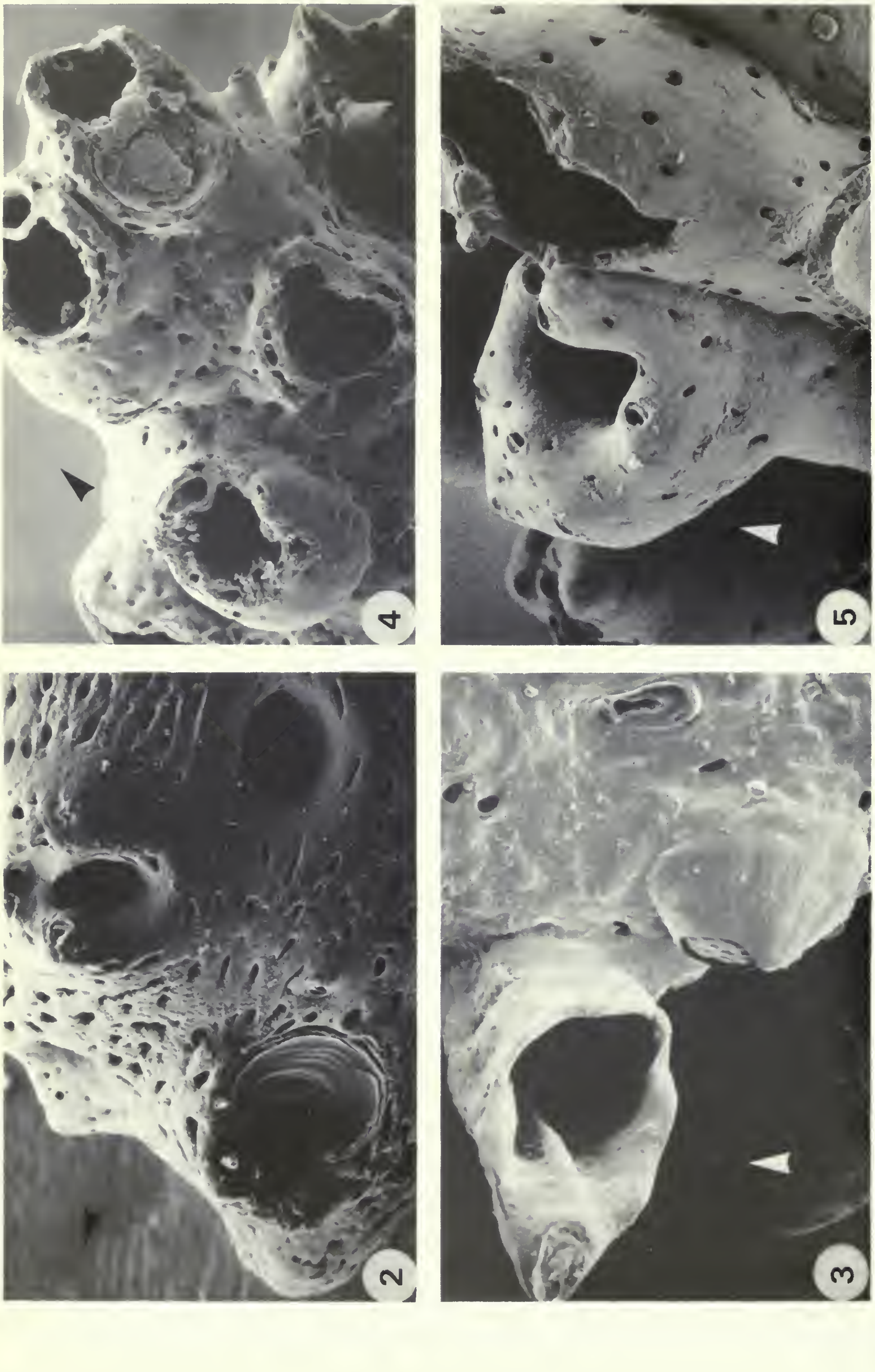


Fig. 1 Diagrammatic, idealised longitudinal section through axis of an erect branch of Lekythoporidae (based on *Lekythopora* and *Poecilopora*). Direction of colony growth (astogenetically distal), arrow at right. External cuticles only shown (thin lines); Primary calcification (thick lines); secondary and extrazooidal calcification stippled; *as* ascus; *ax* axial frontal septulae; *b* topographically distal, frontal bud; *ec* extrazooidal coelom (derived from amalgamation of hypostegal coelom of several zooids); *hc* hypostegal coelom; *ia* interzooidal, frontally budded avicularium; *m* mandible; *o* brood chamber within peristomial ovicell; *op* operculum (direction of opening arrowed); *p* peristome; *pa* peristomial avicularium; *ps* peristomial frontal septula; *t* tube connecting peristomial avicularium with frontal septula; *ts* tentacle sheath.



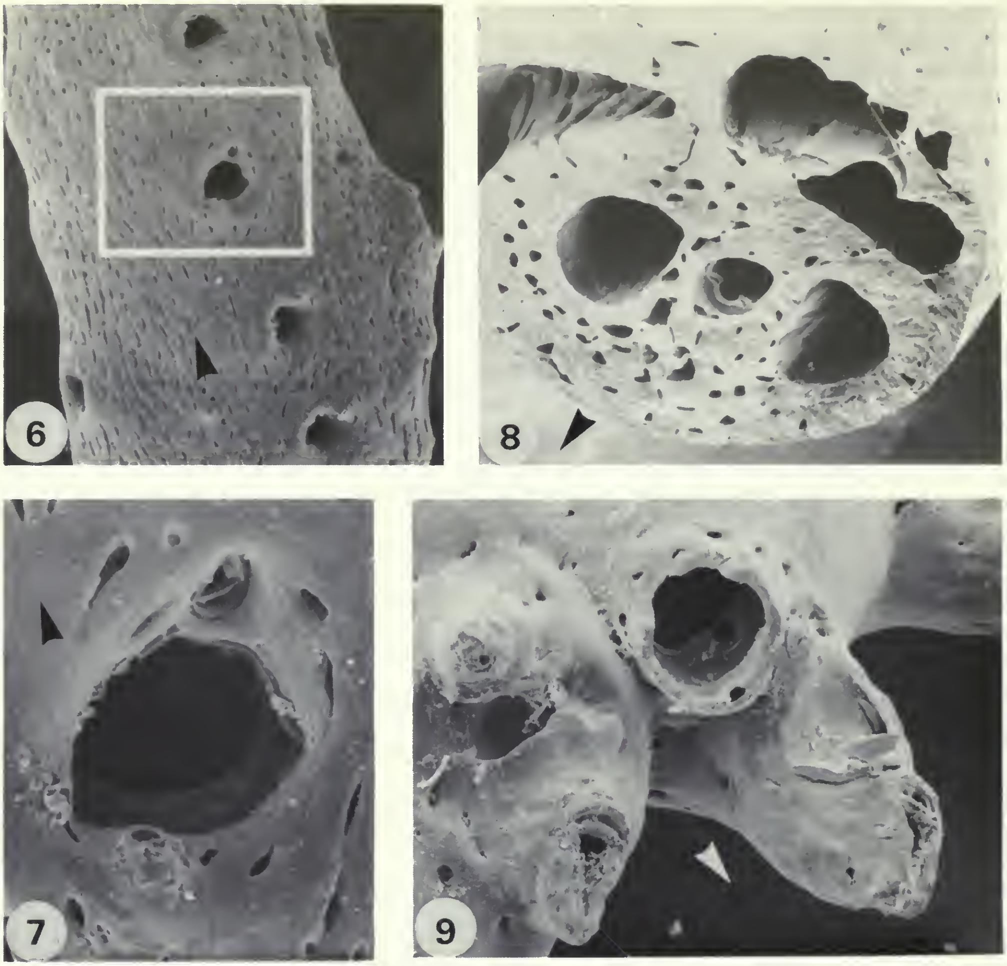
Figs 2–5 Scanning electron micrographs of ovicells of Lekythoporidae; arrows indicate direction of colony growth: (2) *Catadysis immersum* (Busk) BMNH 1963.2.12.247, Montevideo, growing tip with developing ovicell (left) and complete ovicell (right). Note rapid extrazooidal thickening of frontal shields and slit-like frontal pores ×80; (3) *Poecilopora anomala* MacGillivray BMNH 1888.11.14.291, Port Phillip Heads, marginal zooid with elongated peristome and terminal avicularium (left) and ovicell with frontal area ×200; (4) *Turritigera stellata* (Busk) BMNH 1897.12.9.520B, Montevideo, growing tip with developing ovicell (right) and complete ovicells ×90; (5) *Orthoporidra solida* (Busk) BMNH 1899.7.1.3525, S.W. Australia, ovicell with avicularia ×57.

Septulae are present in the axially directed 'concealed' part of the shield, and in the outwardly directed part. This, together with the circumoral region forms the equivalent of the 'exposed' part of the frontal shield in conescharelliniform colonies with 'reversed frontal' budding (see Cook & Lagaaij, 1976, and Fig. 1). One or more circles of septulae surround the primary orifice. The septulae allow the expansion of hypostegal coelom axially to form new zooid buds, and peripherally to allow thickening of the exposed frontal shield calcification and, or, the budding of peristomial or interzooidal avicularia and kenozooids. The primary orifice is terminal, and is orientated with the proximal edge of the operculum directed axially and in a more 'distal' position, with respect to the direction of growth of the branch, than the outwardly directed (morphologically) distal edge (see Fig. 1). This is because the longitudinal axes of the zooids are curved towards the outside of the branch. The peristome arises as a ridge between the circum-oral septulae and other frontal septulae. It becomes tubular and often very elongated, continuing the outward curve of the zooid axis. The ovicell is an expanded diverticulum on the peripheral, morphologically distal, side of the peristome, but the curvature of the zooid and peristome is such that it appears to be topographically 'proximal' in position (see Fig. 1). This illusion is completed in several species when the peristome develops a small secondary 'sinus' on its astogenetically distal, but topographically proximal side (Fig. 18).

The problem of interpreting the relationships of the primary orifice and the ovicell is exacerbated by the length of the peristome and by the rapid development of secondary calcification and frontally budded kenozooids in most species. The hypostegal coeloms may even amalgamate, with the breakdown of interzooidal cuticle, and form extrazooidal coelom with massive extrazooidal calcification. The presence of septulae and extension of hypostegal coelom on the outer sides of the peristome also assists this calcification. The exposed frontal shields, peristome and even ovicells sometimes become completely obscured within only two astogenetic generations of the growing edge or tip of the branch (Fig. 2).

Longitudinal and transverse sections reveal details of the relationships of zooid budding and communication, but because most zooidal axes are curved in more than one plane, complete axial sections cannot be obtained. In colonies with regularly cylindrical branches, *Catadysis,* or irregular cylindrical extensions, *Lekythopora* and *Orthoporidra,* all zooid orifices are orientated with their proximal edges pointing axially and nearly vertically, i.e. in the direction of growth. In colonies which appear superficially to be composed of two 'laminae' of zooids, *Poecilopora*, the proximal sides of orifices of one 'lamina' are directed towards those of the opposing 'lamina', in the same manner as those of the erect, but rooted genus *Flabellopora* (see Harmer, 1957). In colonies with rounded branches with one 'frontal' surface, *Turritigera,* the zooidal axes are twisted as well as curved, but the proximal edges of the orifices are directed towards the axis of the branch. The 'basal' side of these colonies is entirely composed of extrazooidal calcification (Fig. 8).

Avicularia occur on the edge of the peristome in all species. They are derived from circum-oral frontal septulae, and one proximo-lateral avicularium at least is always present, although several may occur. A long, tubular connection between the avicularian chamber and the originating septula passes through the peristomial calcification. This often traces a curved path, which perhaps reflects the distortions in zooidal axes which occur during calcification of the bud. Sometimes the avicularia are raised on long hollow processes, which may bear small secondary avicularia laterally as well as terminally. The long processes become obscured during later thickening, leaving the avicularia at the surface of the branch, where they may appear to be frontally budded interzooids. In addition, large frontally budded, interzooidal avicularia also develop later in astogeny, especially at the bases of branches. The apparently 'confused' budding pattern (especially in *Lekythopora* and *Orthoporidra*), and the effects of extrazooidal calcification therefore make it difficult to distinguish the origins of avicularian types except near the growing tips. Similar difficulties in the genus *Turbicellepora* have been described by Hayward (1978), who also discussed the descriptive terminology applicable to the large 'spatulate' avicularian rostra which often occur in 'celleporine' forms. Measurements of zooids are also difficult to define and obtain, because



Figs 6–9 Scanning electron micrographs of orifices of Lekythoporidae; arrows indicate direction of colony growth: (6) *Catadysis immersum* (Busk) BMNH 1963.2.12.247, Montevideo, part of branch showing secondary orifices and frontal pores ×26; (7) *C. immersum*, secondary orifice with avicularia. Note astogenetically distal (topographically proximal) edge of primary orifice at lower level ×130; (8) *Turritigera reticulata* sp. nov. BMNH 1890.4.16.2A, Marion Island, broken edge of branch from distal side showing one primary orifice (centre), zooid cavities, and thick 'basal' extrazooidal calcification of branch ×57; (9) *T. fenestella* sp. nov. BMNH 1890.4.16.2B, Marion Island, detail of zooid at branch tip, showing sinuate primary orifice, secondary orifice and large avicularium ×112.

the shape of zooids is often irregular, the primary orifice is completely hidden and secondary calcification obscures all limits of structures. One measure of the relative length of zooids may be the distance between the centres of secondary orifices in distal series, but this is very susceptible to error if peristomes are worn or broken. Opercula and primary orifices may often be visible in broken branches, and examination from the topographically 'proximal' (zooid interior) side may reveal differences in shape between them.

Systematic Section

LEKYTHOPORIDAE Levinsen

Lekythoporidae Levinsen, 1909 : 89, 383.

TYPE GENUS. *Lekythopora* MacGillivray.

DESCRIPTION. The characters of the family are redefined as follows. Colonies erect or semi-erect, arising from a small encrusting base which becomes strengthened by frontally budded kenozooids, avicularia and, or, extrazooidal calcification later in astogeny. All zooids of the secondary zone of change and repetition (see Boardman *et al.*, 1969) are frontally and interzooidally budded. Zooids columnar, with a centrally placed, terminal primary orifice. Proximal sides of orifices and asci orientated towards the central axis of the branch. All vertical calcified walls formed as an interior, cryptocystidean shield; axial part concealed, peripheral part and circum-oral region exposed. Shield with a hypostegal coelom and frontal septulae, some of which form a circum-oral ring. Primary calcified orifice straight, curved or sinuate proximally, surrounded by a raised, tubular peristome. Avicularia arising from circum-oral septulae, occasionally numerous, always one proximo-laterally, which appears to be topographically distal. Subrostral chambers terminal, on the edge of the peristome or a mucronate process arising from the peristome. Rostra acute or rounded, mandible slung on a complete bar. Subrostral chamber connected to the originating septula by a long tube, which passes through the calcified wall of the peristome. Interzooidal, frontally budded avicularia sporadic, variously orientated, mandible slung on a complete bar, which may bear a ligula. Brood chamber protected by a large, globular peristomial ovicell, sometimes with an exposed, frontal cuticular area, or with pores and small avicularia on its surface.

REMARKS. The family has been defined (e.g. by Bassler, 1953) to include the genera *Lekythopora* MacGillivray, *Poecilopora* MacGillivray, *Turritigera* Busk, *Catadysis* Canu & Bassler, *Orthoporidra* Canu & Bassler and *Actisecos* Canu & Bassler. Of these, all but *Actisecos* have been described as having 'proximal' ovicells. *Actisecos,* a rooted, lunulitiform genus, has little in common with the other genera and was assigned to the family Actisecidae by Harmer (1957 : 854). The remaining genera differ from each other principally in details of budding pattern, the shape of the primary orifice and operculum, and the characters of avicularia and ovicells.

Most of the specimens examined are small, rarely more than 10–15 mm in height, and type material is often worn and fragmentary. A few colonies, *C. immersum, O. compacta, T. reticulata* and *T. fenestella,* are relatively large and exceed 50 mm in height or width. Some species show distinct substratum preferences. *Lekythopora* is often found on erect hornerid and adeonid bryozoans, *Poecilopora* on flexible cellariiform and cellulariiform bryozoans or on hydroids, *Turritigera* is often associated with other bryozoans or with polychaete tubes, and colonies of *Orthoporidra* may originate on small stones.

With one exception, *Poecilopora cribritheca,* all species are from the Southern hemisphere, and perhaps apart from *Lekythopora,* are from fairly deep, sometimes very deep, cold waters. Generally, bottom temperatures have been given only for Antarctic localities in published data, and those for low latitude, 'tropical' and 'subtropical' specimens are not known (see Table 2). Several Antarctic species have been reported as abundant, but material examined here, from the Zoological Museum Amsterdam (ZMAC), the National Museum of Victoria (NMV), the British Museum (BMNH), and the Manchester Museum (MM) collections, is not generally plentiful. In view of the enormous, but unworked collections which have been made from the Antarctic shelf, and the increasing number of species becoming known from deep waters, it should be possible, theoretically at least, to obtain larger quantities of some of the species described here, and to analyse their population variation in colony form and zooidal morphology. Several species appear to belong to complexes, composed of widely distributed populations, each with different character correlations. Additional information on early astogeny, and internal features such as tentacle

Table 1 Average measurements of zooids of Lekythoporidae (in mm)

	Lz	lz	Lpo	lpo	Lov	lov
L. hystrix	0·70	0·40	0·12	0·11	0·20	0·40
P. anomala	0·40	0·28	0·08	0·07	0·15	0·20
P. cribritheca	0·50	0·30	0·12	0·11	0·18	0·20
T. stellata Stn 320	0·50	0·30	0·13	0·16	0·20	0·25
T. stellata Stn 142	0·60	0·35	0·13	0·18	0·25	0·35
T. reticulata	1·20	0·50	0·13	0·11	0·40	0·50
T. fenestella	0·75	0·35	0·17	0·12	0·25	0·30
C. immersum	0·65	0·50	0·12	0·17	0·25	0·35
O. compacta	0·80	0·50	0·19	0·23	0·40	0·50
O. solida	1·20	0·50	0·20	0·25	0·40	0·50
O. petiolatus	0·60	0·33	0·12	0·13	0·24	0·30

Table 2 Nominal Recent records of Lekythoporidae and *Orthoporidroides*. Additional temperature data from Murray, 1895 and Livingstone, 1928; estimated depths and temperatures in parentheses

Species	Locality data	Latitude	Longitude	Depth (metres)	Temperature (°C)	Reference
Lekythoporidae						
L. hystrix	Port Phillip Heads	38°30′S	144°30′E	(60)	(+17)	BMNH
L. hystrix	Port Western	38°30′S	145°30′E			BMNH
L. hystrix	Port Jackson	34°S	151°E	(60)	(+17)	BMNH
L. avicularis	Port Jackson	34°S	151°E	146	(+17)	Maplestone 1909
P. anomala	Port Phillip Heads	38°30′S	144°30′E	(60)	(+17)	BMNH
P. anomala	Twofold Bay	36°59′S	150°20′S	275	(+12·8)	BMNH
P. anomala	Maria Island	42°37′S	148°E	73		Thornely 1924
P. cribritheca	Sulu Archipelago	6° 8′N	121°19′E	275	(+12)	Harmer 1957
T. stellata	Montevideo	37°17′S	53°52′W	1100	+2·8	Busk 1884
T. stellata	Cape of Good Hope	35°04′S	18°37′E	275	+8·3	Busk 1884
T. stellata	Cape Horn	53°S	68°W			Waters 1905
T. stellata	Is. Topar	50°8·5′S	74°41′W	360		Moyano 1974
T. stellata	Caleta Hale	47°57′S	74°41′W	40–50		Moyano 1974
T. stellata	Bellinghausen Sea	70°S	80°48′W	?500	+0·9	Waters 1904
T. stellata	Bellinghausen Sea	70°20′S	83°23′W	459	+0·8	Waters 1904
T. stellata	Bellinghausen Sea	70°15′S	84°6′W	659	+0·8	Waters 1904
T. stellata	Bellinghausen Sea	70°23′S	82°47′W	480	+0·8	Waters 1904
T. stellata	Bellinghausen Sea	71°14′S	89°14′W	460	−0·3	Waters 1904
T. stellata	Bellinghausen Sea	71°18′S	88°2′W	435	−0·3	Waters 1904
T. reticulata	Marion Island	38°S	46°40′W			BMNH
T. fenestella	Marion Island	38°S	46°40′W			BMNH

Continued

Species	Locality data	Latitude	Longitude	Depth (metres)	Temperature (°C)	Reference
T. spectabilis	Uruguay	36°49′S	53°15·4′W	1661–1679		d'Hondt 1981
		38°16·9′S	51°56·1′W	4382–4402		d'Hondt 1981
		36°55·7′S	53°01·4′W	2707		d'Hondt 1981
C. immersum	Montevideo	37°17′S	53°52′W	1100	+2·8	Busk 1884
C. immersum	Burdwood Bank	54°25′S	57°32′W	103		Hayward 1980
O. compacta	Bellinghausen Sea	70°S	80°48′W	?500	+0·9	Waters 1904
O. compacta	Bellinghausen Sea	71°18′S	88°02′W	435	−0·3	Waters 1904
O. compacta	Bellinghausen Sea	71°19′S	87°37′W	436	−0·2	Waters 1904
O. compacta	Halley Bay	75°31′S	26°36′W			BMNH
O. compacta	Scotia Bay	61°S	45°W			BMNH
O. compacta	McMurdo Sound	77°05′S	164°17′E	256		BMNH
O. compacta?	South Chile	62°28·5′S	59°41·5′W	119		BMNH
O. compacta?	Queen Maude Land	70°19·4′S to 70°20·9′S	24°12·6′E to 24°13·4′E			Redier 1965
O. setosa	Commonwealth Bay	64°32′S	97°20′E	201		Thornely 1924
O. setosa	Commonwealth Bay	66°08′S	94°17′E	220		Thornely 1924
O. setosa	Adelie Land	66°55′S	145°21′E	782	+1·8	Thornely 1924
O. setosa	Adelie Land	66°32′S	141°39′E	287	+1·62	Thornely 1924
O. setosa	Graham Land	65°S	64°W	750		Vigeland 1952
O. setosa	Graham Land	65°S	64°W	90		Vigeland 1952
O. setosa	Graham Land	65°S	64°W	140		Vigeland 1952
O. petiolata	Cape Horn	53°13′S	68°31′W	97	+6·6	Waters 1905
O. petiolata	Burdwood Bank	54°25′S	57°32′W	103		Hayward 1980
O. petiolata	Houtjes Bay	34°10′S	18°10′E			BMNH
O. solida	S. W. Australia	42°42′S	134°10′E	4758	+1·1	Busk 1884
Orthoporidroides						
O. erectus	Magellan Straits	55°S	72°W	320	(+7·8)	BMNH
O. erectus	Montevideo	37°17′S	53°54′W	1100	+2·8	BMNH
O. erectus	Is. Innocentes	50°33′S	74°53′W	150		Moyano 1974
O. erectus	Is. Topar	50°8·5′S	74°41′W	360		Moyano 1974
O. erectus	Canal Zenteno	52°49′W	73°40′S	30–40		Moyano 1974
O. aff. *erectus*	E. Falkland Is.	52°09′S	58°14′W	79	+8·3	BMNH
O. aff. *erectus*	E. Falkland Is.	50°29′S	58°52′W	140	+4·78	BMNH
O. aff. *erectus*	E. Falkland Is.	50°30′S	58°19′W	141	+5·4	BMNH
O. aff. *erectus*	E. Falkland Is.	52°31′S	58°29′W	146	+5·45	BMNH
O. aff. *erectus*	E. Falkland Is.	50°50′S	57°13′W	144	+5·61	BMNH
O. robusta	Chile	37°37′S	73°40′W	600		Moyano 1981

number, opercular variation etc., should result in a better understanding of the systematic relationships within the Lekythoporidae, and the relationships of the family with other ascophoran groups.

LEKYTHOPORA MacGillivray

Lekythopora MacGillivray, 1883 : 194.

Type species. *L. hystrix* MacGillivray.

DESCRIPTION. Colonies forming short, irregularly cylindrical branches. Zooids with several series of frontal septulae. Primary orifice sinuate, operculum extended proximally but not distinctly sinuate. Ovicells with a frontal, marginally porous area covered by cuticle.

REMARKS. *L. hystrix* appears to be the only species referable to the genus. Harmer (1957 : 884) referred *Phylactella lucida* Hincks to *Lekythopora*; this species has been discussed by Cook (1968 : 220) and referred to *Celleporina. L. perplexa* Harmer (1957 : 884, pl. 59, figs. 5–7, 10) is also a 'celleporine' species with 'normal' frontal budding and tabulate ovicells and may be provisionally referred to *Celleporina.* Harmer (1957 : 885) also mentioned an unnamed species of *Lekythopora* from Japan. Examination of his specimens shows that these colonies, too, are referable to *Celleporina. L. laciniosa* Calvet (1907 : 445, pl. 29, figs. 13, 14) is attributable to *Celleporina.*

Lekythopora hystrix MacGillivray

Lekythopora hystrix MacGillivray, 1883 : 194, pl. 2, figs. 6, 6a–d; 1885 : 113, pl. 2, fig. 6: 1888 : 201, pl. 156, figs. 4–10; 1895: 106, pl. 14, figs. 1–2. Waters, 1885 : 308. Brown, 1958 : 83.
Lekythopora avicularis Maplestone, 1909 : 273, pl. 78, fig. 12.

SPECIMENS EXAMINED. BMNH, Port Phillip Heads, Victoria, 1897.5.1.934,937, 1899.5.1.1328, 1934.10.20.103. Port Western, S. Australia, 1934.2.20.23. Australia, 1883. 10.15.125–145. Port Jackson, Sydney, 1981.4.1.1. NMV, Port Phillip Heads 64611, 64612 (fig'd MacGillivray, 1888) and 64602.

DESCRIPTION (Figs. 14a, 15). Primary zooids with short peristomes, frontally budded zooids with long, curved peristomes, directed peripherally, sometimes with a secondary, topographically proximal, sinus. Peristomal avicularia with curved, acute rostra, placed on the edge of the peristome. Interzooidal avicularia elongated, only slightly expanded and rounded terminally, orientated proximally to branch growth. Ovicell with frontal area surrounded by minute pores.

REMARKS. MacGillivray (1888 : 211) noted that the primary orifice was difficult to see, and described it variously as 'rounded' (1883) or 'with a notch in the lower lip' (1888). In one illustration (1885, pl. 2, fig. 6), he actually figured the relationship of the proximal sinus with a distally placed ovicell, but apparently did not notice that this orientation was in contradiction to his description of the ovicell as 'proximal'. However, he was aware of the reversal of orifice orientation with respect to direction of growth in *P. anomala,* and compared it with that of *L. hystrix.* The relationships of *L. mooraboolensis* Maplestone (1902 : 25, pl. 2, fig. 18) and *L. kitsoni* Maplestone (1902 : 25, pl. 2, fig. 19), from the Australian Tertiary, are difficult to evaluate without specimens. *L. mooraboolensis* was described from a single, small, globular specimen of 3–4 zooids and may have been the young astogenetic stage of a colony of *Conescharellina. L. kitsoni* was described as ligulate and bilaminar and appears to have had 'proximal' ovicells with a frontal area. It may be assignable to either *L. hystrix* or *P. anomala* (see below).

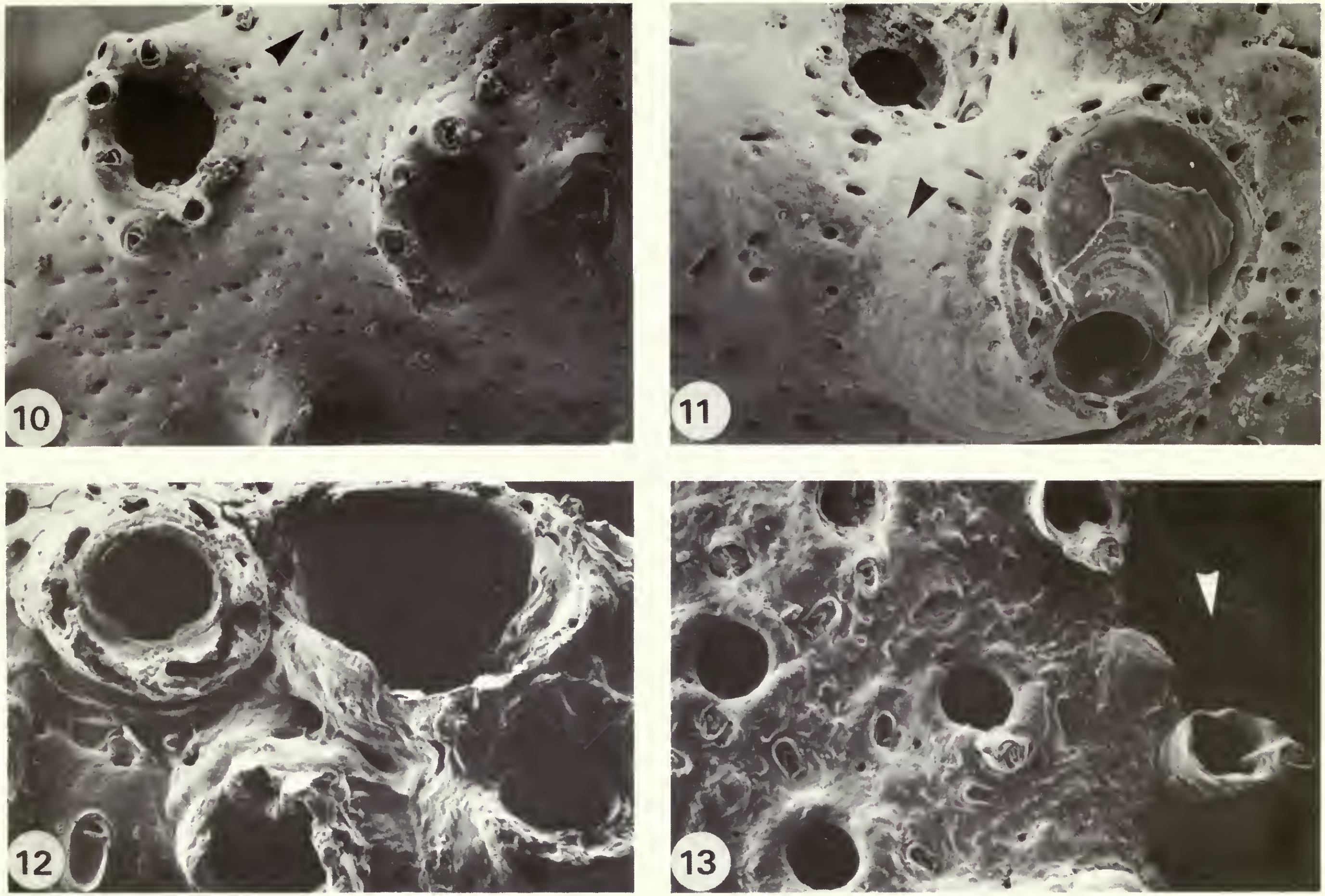
Apart from *L. kitsoni, L. hystrix* is apparently the only species of the family which has a fossil record. Both Waters (1885) and MacGillivray (1895) noted its occurrence from several Tertiary Australian localities (see also Brown, 1958).

POECILOPORA MacGillivray

Poecilopora MacGillivray, 1886 : 136.

TYPE SPECIES. *P. anomala* MacGillivray.

DESCRIPTION. Colonies with compressed, cylindrical, or 'bilaminar' branches, bifurcating in one plane. Zooids in opposing interdigitating series. Primary orifice sinuate, operculum extended proximally but not sinuate. Ovicells with a frontal area covered by cuticle, visible late in ontogeny.



Figs 10–13 Scanning electron micrographs of orifices of Lekythoporidae; arrows indicate direction of colony growth: (10) *Turritigera stellata* (Busk) BMNH 1897.12.9.520B, Montevideo, secondary orifices with terminal peristomial avicularia ×70; (11) *T. reticulata* sp. nov. BMNH 1890.4.16.2A, Marion Island, primary orifices and developing ovicell ×80; (12) *Poecilopora anomala* MacGillivray BMNH 1888.11.14.291, Port Phillip Heads, interdigitating, opposing zooid series at growing edge, showing primary orifices ×130; (13) *P. anomala* secondary orifices, showing elongated marginal peristome, immersed central peristomes, peristomial and interzooidal avicularia ×80.

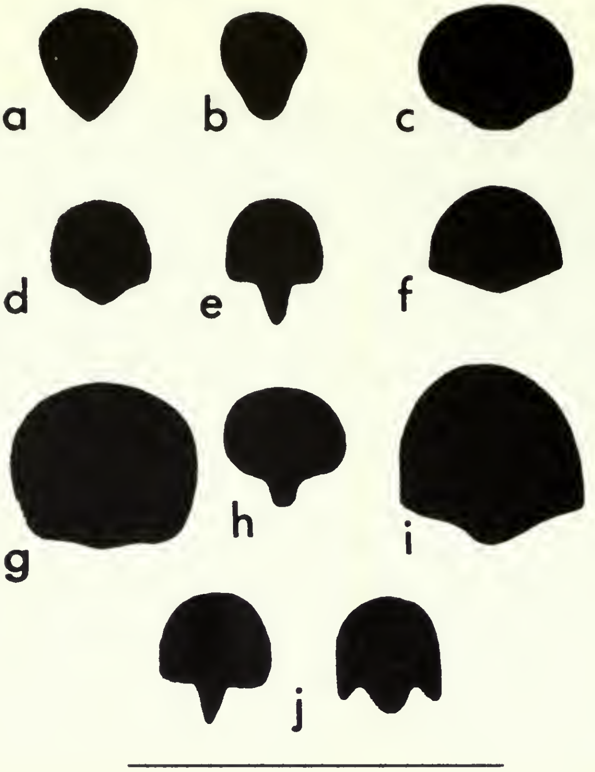


Fig. 14 Silhouettes of opercula of Lekythoporidae and *Orthoporidroides*, Scale bar = 0·50 mm; (a) *Lekythopora hystrix*; (b) *Poecilopora cribritheca*; (c) *Turritigera stellata*; (d) *T. reticulata*; (e) *T. fenestella*; (f) *Catadysis immersum*; (g) *Orthoporidra compacta*; (h) *O. petiolatus*; (i) *O. solida*; (j) *Othoporidroides erectus.*

Poecilopora anomala MacGillivray

Poecilopora anomala MacGillivray, 1886 : 136, p. 1, fig. 9; 1888 : 211 (as *P. anomola*), pl. 156, figs. 11–13.

?*Turritigera stellata* Thornely (not Busk), 1924 : 18.

Specimens examined. BMNH, Port Phillip Heads, 1887.12.10.67, 1888.11.14.103,134,291, 1897.5.1.947.948,949, 1889.7.1.3613. Port Western, South Australia, 1899.7.1.5129. *Challenger* Stn. 163A, Twofold Bay, New South Wales, 220 m, 1899.7.1.4081, 1963.2.12.15.

Description (Figs. 3, 12, 13) The small colonies rarely exceed a height of 10 mm, and are branched in one plane. The 'bilaminar' growth resembles that of *Flabellopora.* The primary orifice has an indistinct sinus proximally. Zooids small, with porcellanous frontal shields with scattered septulae. Peristomes long at lateral margins of colony, flaring terminally; short elsewhere, with one acute avicularium. Interzooidal avicularia short, slightly expanded, and rounded terminally, randomly orientated. Ovicells prominent even late in ontogeny, protruding beyond the secondary thickening, frontal area surrounded by minute pores.

Remarks. The early stages of the colony may consist of the ancestrula and one encrusting zooid generation only (1899.7.1.3613).

MacGillivray (1886 : 137) noted that the reversal of orifice orientation was the explanation for the apparently 'proximal' ovicells, and postulated that *L. hystrix* might have a similar structure.

Thornely's (1924) record of '*Turritigera stellata*' was not from an Antarctic locality. Although most of the stations mentioned in her paper were from Wilkes Land, Antarctica, the locality 'Maria Island' (42°37′S, 148°E, 73 m) is Tasmanian (see Livingstone, 1928 : 8). Thornely noted that her colonies were 'bilaminar', that the zooids had tubular peristomes with only one marginal avicularium, and that the ovicells had a perforated frontal area. The locality of her specimens indicates that they were either *L. hystrix* or *P. anomala,* and the colony form suggests strongly that they were the latter.

The specimens from *Challenger* Stn 163A were not described by Busk (1884). The other bryozoans from this Station include a large number of cellariiform and cellulariiform species, which provide substrata for the colonies of *P. anomala.*

Poecilopora cribritheca (Harmer)

Catadysis cribritheca Harmer, 1957 : 886, pl. 59, figs 9, 12–15, 22, 23.

SPECIMENS EXAMINED. ZMA, LECTOTYPE, Siboga Stn 105, Sulu Archipelago, 275 m. BMNH, Paralectotype, as above, 1981.5.6.1.

DESCRIPTION (Fig. 14b). Colonies with compressed cylindrical branches. Primary orifice with a wide sinus. Zooids with porcellanous calcification and scattered frontal septulae. Peristomial avicularia not protuberant, rounded or subtriangular. Ovicell immersed, but the frontal area, which has minute, slit-like pores, remains visible.

REMARKS. Harmer (1957) assigned *P. cribritheca* to *Catadysis,* which has cylindrical branches of zooids without long peristomes but with numerous frontal pores. The porcellanous calcification, compressed branches, long peristomes and exposed frontal area of the ovicells of *P. cribritheca* are all characters typical of *Poecilopora.*

P. cribritheca differs from *P. anomala* in its slightly larger zooids, and the shape and distribution of the avicularia. Interzooidal avicularia seem to be absent, but the material is fragmentary, and incomplete. *P. cribritheca* is the only species of Lekythoporidae known to occur in the tropical waters of the Northern hemisphere, but is from fairly deep water (275 m) near the equator.

TURRITIGERA Busk

Turritigera Busk, 1884 : 129.

TYPE SPECIES. *T. stellata* Busk.

DESCRIPTION. Colonies with cylindrical branches, sometimes becoming reticulate with anastomoses. Most zooids curved so that their peristomes open on one side of the branch. Branches dichotomous or formed by frontally budded zooids arising in groups at right angles to the primary branch, in more than one plane. Primary orifice sinuate, but operculum curved or sinuate proximally. Peristomial avicularia sometimes numerous, occurring on the edge of peristomes, often on raised processes. Ovicell rapidly occluded by secondary calcification, but often remaining prominent.

Turritigera stellata Busk

Turritigera stellata Busk, 1884 : 130, pl. 24, fig. 1. Waters, 1888 : 22, pl. 1, figs. 22, 25; 1904 : 76, pl. 5, fig. 3, pl. 8, fig. 13; 1905 : 242, pl. 29, figs. 19, 20. Moyano, 1974 : 18, figs. 4, 8, 31–34.
not *Turritigera stellata* Thornely 1924, see *P. anomala.*

SPECIMENS EXAMINED. BMNH, *Challenger* Stn. 320, 1100 m, 1887.12.9.517.520B, 1899.7.1.3166,3167, 1944.1.8.240,241. *Challenger* Stn. 142, 275 m, 1887.12.9.518,519, 1899.7.1.498,499,500, 1934.2.16.13, 1944.1.8.239,242. Locality? New Zealand, 1936.12.30.155.
MM, *Challenger* Stn. 320, T38–40; Expedition Antarctique Belge, T17–37.

DESCRIPTION (Figs. 4, 10, 14c). Colonies reaching a height of 20–30 mm, branched irregularly. Primary orifice with a small, rounded proximal sinus, operculum with a distal flange, curved proximally. Zooids with numerous frontal septulae, which become slit-like as calcification increases. Peristomes long, flaring terminally, with one to seven terminal avicularia, which are sometimes raised on short processes. Mandibles and rostra acute. Interzooidal avicularia elongated, slightly expanded and rounded terminally, randomly orientated, sometimes present on non-zooidal 'basal' side of colony. Ovicell with a small frontal area which is rapidly obscured by frontal thickening. 18 tentacles (Waters). 'Basal' thickening extrazooidal, with slit-like pores and minute avicularia.

REMARKS. The South American (Stn. 320), South African (Stn. 142) and Antarctic populations show some differences in characters. Colonies from Stn. 320 are rather delicate, with numerous small peristomial avicularia, and interzooidal avicularia on the 'frontal' and 'basal' sides. There is relatively little extrazooidal thickening (see also Moyano, 1974). Colonies from Stn. 142 are at a later stage of ontogenetic development and consist of astogenetically earlier fragments. They appear more robust, with considerable 'basal' and 'frontal' thickening. The axially directed, proximal, peristomial avicularium is large and the remainder are reduced in number, usually to two or three. Interzooidal avicularia are absent. Colonies from Waters's (1904) Antarctic Stations are very robust, and the zooids tend to be arranged biserially (c.f. *T. reticulata*). Waters noted that some colonies possessed anastomoses (1904, pl. 5, fig. 3a). The zooids have numerous peristomial avicularia, but interzooidal avicularia are very rare. In contrast, specimens from ?New Zealand (locality doubtful) are delicate but have one enlarged peristomial avicularium, like those from South Africa. *T. stellata* would therefore appear to be a very variable species. The extent and significance of this variation can only be assessed when complete colonies, showing all astogenetic and ontogenetic stages can be compared from a wide range of populations. Recently, for example, d'Hondt (1981 : 41, pl. 5, figs. 1–3) has described a new, abyssal form, *T. spectabilis,* from a depth range of 1661–4402 m, off Uruguay. *T. spectabilis* resembles some forms of *T. stellata* in having only one, large peristomial avicularium. Ovicells were absent.

The operculum of *T. stellata* figured by Waters (1904, pl. 5, fig. 3b) was distinctly sinuate, like the primary orifice. Waters's preparation of opercula (MM T33) is badly preserved and no sinus is visible. None of the numerous opercula in the Busk preparations from South African material (BMNH 1899.7.1.498,499) shows any sinus.

Turritigera reticulata sp. nov.

SPECIMENS EXAMINED. BMNH, HOLOTYPE and Paratypes, all parts of one colony, Marion Island, 1890.4.16.2A.

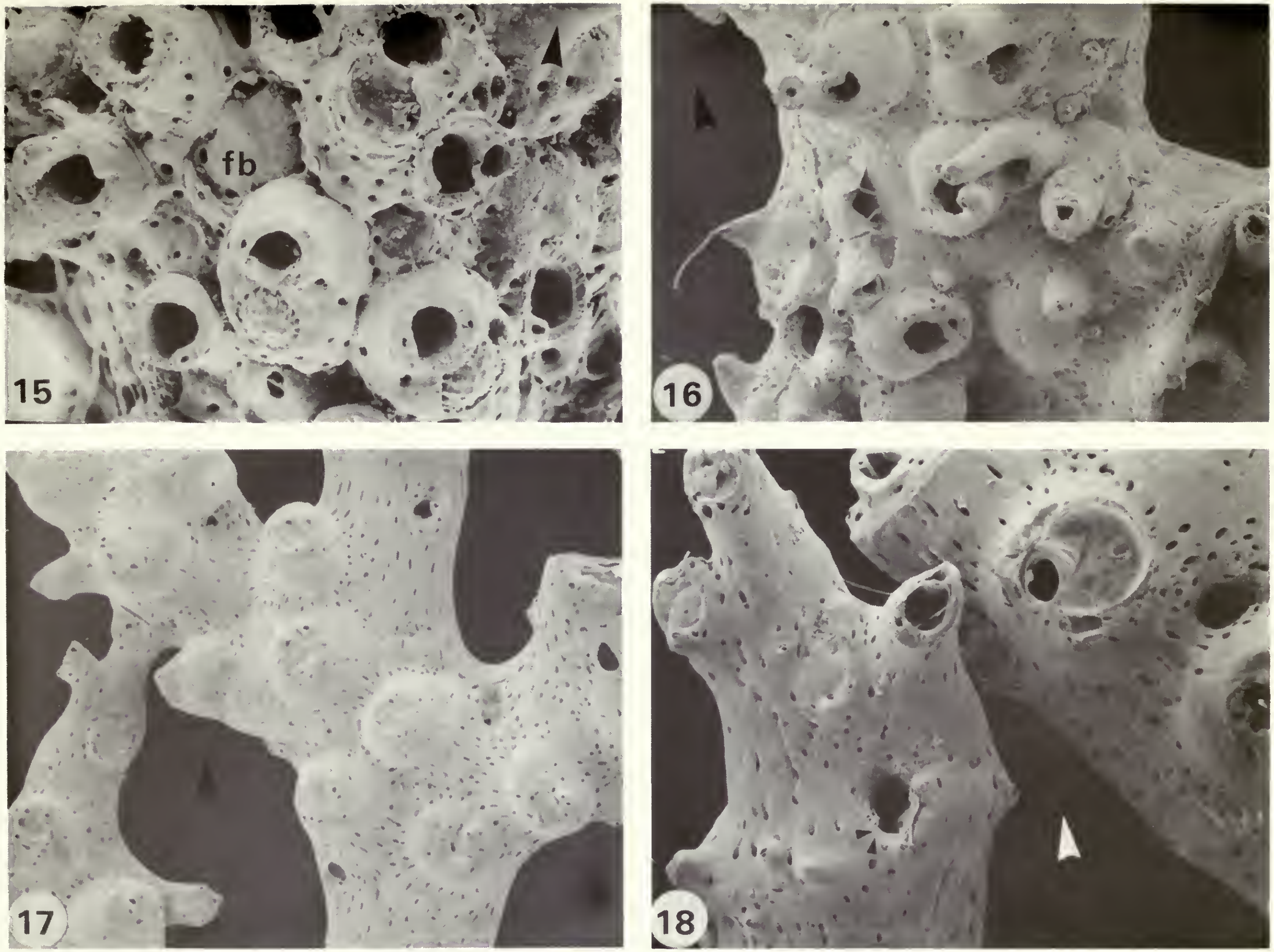
ETYMOLOGY. *Reticulatus* (L)—net-like, referring to the colony form.

DESCRIPTION (Figs. 8, 11, 14d, 17, 18). Colonies large, 50 mm in height, reticulate, with anastomosing branches. Zooids very large, alternating and biserial, peristomes short. Primary orifice very small, with a fairly wide sinus, operculum distinctly sinuate. Secondary orifice often forming a topographically proximal sinus. Frontal pores numerous, becoming slit-like. Peristomial avicularia small, one to three are bourne on a stout suboral, topographically distal process, mandibles short, triangular. Interzooidal avicularia absent. Ovicells very large, with marginal pores; prominent at first, becoming partially obscured by extrazooidal thickening, often orientated medially.

REMARKS. The reticulate growth form of *T. reticulata* is shared by *T. fenestella* (see below) and, according to Waters (1904), by some colonies of *T. stellata.* The large zooidal dimensions of *T. reticulata,* together with its very small primary orifice distinguish it from *T. fenestella.*

Turritigera fenestella sp. nov.

SPECIMENS EXAMINED. BMNH, HOLOTYPE and Paratypes, all parts of one colony, Marion Island, 1890.4.16.2B.



Figs 15–18 Scanning electron micrographs of Lekythoporidae; arrows indicate direction of colony growth: (15) *Lekythopora hystrix* MacGillivray BMNH 1883.10.15.125–145, Australia, zooids with topographically proximal ovicells, note developing frontal bud (*fb*) ×55; (16) *Turritigera fenestella* sp. nov. BMNH 1890.4.16.2B, Marion Island, zooids with ovicells, note median and lateral orientation ×36; (17) *T. reticulata* sp. nov. BMNH 1890.4.16.2A, Marion Island, part of colony from 'frontal' side showing anastomosis, note early closure of ovicelled zooids ×20; (18) *T. reticulata*, zooids showing relatively late ovicell development, and secondary (topographically proximal) 'sinus' (small arrows) ×37.

ETYMOLOGY. *Fenestella* (L)—a little window, referring to the colony form.

DESCRIPTION (Figs. 9, 14e, 16). Colony large, 50 mm in height, reticulate, with anastomosing branches. Zooids irregularly arranged, fairly small, with a primary orifice with a proximal plate, in which there is a distinct round sinus; operculum also with a distinct sinus. Frontal pores fairly numerous, rounded, becoming obscured. Peristomial avicularia one to three, one bourne on a very long, curved suboral process. Mandibles triangular, the suboral mandible large, rostrum hooked terminally. Ovicells small, smooth, remaining prominent, although obscured by extrazooidal thickening, often orientated medially.

REMARKS. The similarities in colony form of *T. fenestella* and *T. reticulata,* which were from the same locality, tend to obscure the distinct differences in budding pattern, zooidal size and orificial characters which exist between them. The zooids of *T. fenestella* are similar in size to those of *T. stellata,* but differ completely in the form of the avicularian processes and in the shape of the operculum. The three species described above form a complex, which requires more plentiful material for elucidation.

CATADYSIS Canu & Bassler

Catadysis Canu & Bassler, 1927 : 12, 23, 25.

TYPE SPECIES. *Myriozoum immersum* Busk (=*Schizoporella challengeria* Waters).

DESCRIPTION. Colonies with regularly cylindrical branches, zooids opening on all sides. Zooids with numerous frontal septulae, peristomes not prominent. Primary orifice with a rounded sinus, operculum curved proximally. Peristomial avicularia small, interzooidal avicularia absent. Ovicells imperforate.

Catadysis immersum (Busk)

Myriozoum immersum Busk, 1884 : 170, p. 25, fig. 4.
Schizoporella challengeria Waters, 1888 : 30, pl. 2, figs. 25–28.
Catadysis challengeria (Waters) Canu & Bassler, 1927 : 11, Bassler, 1953 : G233.
Catadysis immersum (Busk) Harmer, 1957 : 885. Hayward, 1980 : 712, figs. 5A–D.

SPECIMENS EXAMINED. BMNH, *Challenger* Stn 320, 1100m, 1887.12.9.683,684,685B, 1899.12.12.18, 1899.7.1.2295, 1934.11.12.57, 1944.1.8.333,334, 1963.2.12.221,247. 'Bruce' Stn 346 (Scottish National Antarctic Expedition) Burdwood Bank, 1936.12.30.297.

DESCRIPTION (Figs. 2, 6, 7, 14f). Colonies large, 50×30 mm, branching in all planes. Zooids with numerous frontal septulae which become immersed by extrazooidal calcification as a series of slit-like pores. Branches cylindrical, smooth, composed of four series of zooids. Peristomes never prominent, orifices rapidly obscured by secondary calcification, leaving rounded pits on the branch surface. Peristomial avicularia small, proximal and distal, mandibles triangular. Ovicells obscured very early in ontogeny.

REMARKS. Waters (1888) introduced the name *'Schizoporella challengeria'* for Busk's species because he considered that it belonged to the genus *Schizoporella* and that the combination was therefore preoccupied by *Onchopora immersa* Haswell (1880), which he also assigned to *Schizoporella. O. immersa* is referable to the genus *Tetraplaria* (see Harmer, 1957 : 1055), and as *Catadysis* has little in common with *Schizoporella,* Waters's name *'challengeria'* is unnecessary (see also Harmer, 1957 : 885, and Hayward, 1980).

Most specimens are small and fragmentary, but one from *Challenger* Stn 320 exceeds 50 mm in width, with numerous branches.

ORTHOPORIDRA Canu & Bassler

Orthopora Waters, 1904 (preoccupied).
Orthoporidra Canu & Bassler, 1927 : 12, 23, 34.

TYPE SPECIES. *Orthopora compacta* Waters.

DESCRIPTION. Colony with irregularly cylindrical branches. Primary orifice usually straight proximally, but opercula may be curved. Zooids with numerous frontal septulae, calcification smooth and very thick. Peristomial avicularia often raised on long, hollow mucronate prominences. Ovicells large, usually imperforate, but with small frontal avicularia.

REMARKS. A large number of specimens has been recorded from many Antarctic and sub-Antarctic localities. These appear to have the general character of *O. compacta* as described below. Small differences in the primary orifice and operculum, however, indicate that population studies are necessary, and it is possible that several distinct species will be found to exist, once plentiful material has been examined.

Orthoporidra compacta (Waters)

Orthopora compacta Waters, 1904 : 75, pl. 5, figs. 4a–i. ?Redier, 1965 : 4, 32.

Orthoporidra compacta: Canu & Bassler, 1927 : 12; 1929 : 515, fig. 214. Rogick, 1965 : 406. Moyano, 1978 : 44.

?*Cellepora setosa* Thornely, 1924 : 17, fig. 5. Livingstone, 1928 : 76, pl. 3, fig. 8, Figs. 18–20. Moyano, 1978 : 44.

?not *Cellepora setosa*: Redier, 1965 : 30; 1966 : 2.

SPECIMENS EXAMINED. MM, T10–15, 343, Waters's (1904) preparations including operculum (T14) and tentacles (T12), Expedition Antarctique Belge. BMNH, Halley Bay, 1966.3.4.4. Bahia, Chile, 1971.3.26.29. Scotia Bay, S. Orkneys, 1920.12.11.3. McMurdo Sound, 1981. 3.1.1.

DESCRIPTION (Figs. 14g, 21, 22). Colonies large, branched in several planes. Primary orifice and operculum slightly curved proximally. Zooids large, frontal septulae distinct, marginal and circum-oral, in two rows across exposed frontal shield. Suboral, topographically distal, avicularium raised on a long tubular process, mandible rounded or triangular, rostrum bar with a ligula. Interzooidal avicularia oval or expanded terminally, rostrum bar with a ligula, usually orientated proximally. Ovicell large with small avicularia on the surface. 24 tentacles (Waters).

REMARKS. The only type material consists of decalcified sections and preparations etc. The operculum (T14) differs from that figured by Waters (1904) and resembles that of *O. solida* in being slightly curved proximally, with lateral proximal lacunae which may be muscle insertions (cf. Waters, 1904).

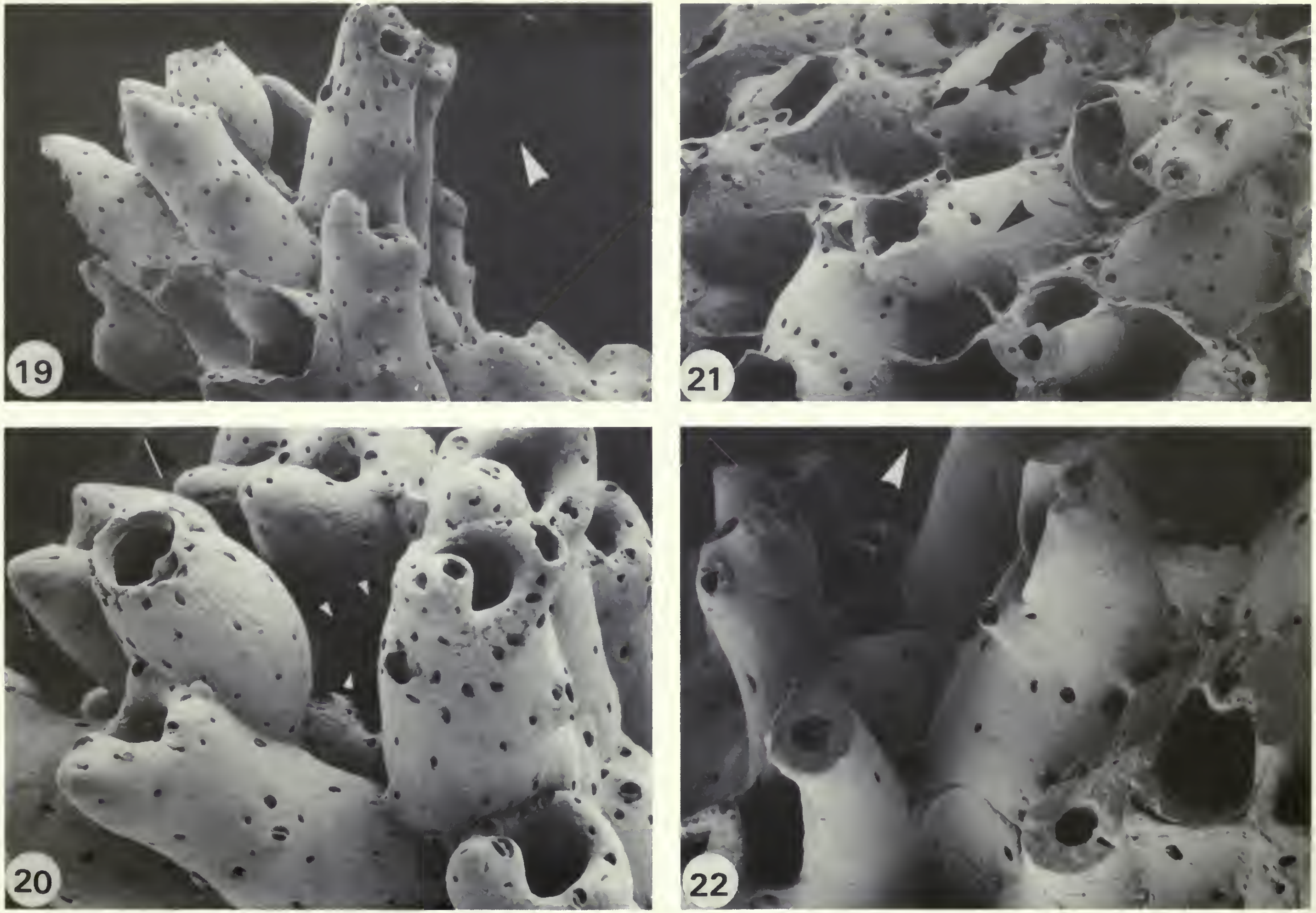
Thornely (1924) introduced *C. setosa* for specimens from several Antarctic localities. Her specimens were redescribed by Livingstone (1928), who noted that neither the primary orifice nor operculum were sinuate. Both authors figured large ovicells with small pores, or avicularia?, on their surfaces.

The only available specimen named as *O. setosa,* which is part of the material described or listed by Redier (1965, 1966), is a bifurcated branch from Antarctica identified by Dr A. B. Hastings (Stn 136, Expedition Antarctique Belge, BMNH 1964.8.2.5.). Although similar to *O. compacta* in most characters including those of the large, wide, ligulate interzooidal avicularia, this specimen differs in the dimensions of the orifice and in possessing a sinuate operculum. The primary orifice is straight proximally but has a small central notch, is longer than wide and generally far smaller than that of *O. compacta. 'C. setosa* Redier' is therefore, in part at least, a separate taxon from *C. setosa* Thornely and *O. compacta.*

Additional material is required before all the Antarctic records of these forms can be reassessed. Redier's (1965) material of *O. compacta* also requires re-examination. His record of the Philippine Islands as a locality for the species is a mistaken reference to the illustrations included by Canu & Bassler (1929) in their paper on Philippine bryozoans.

Orthoporidra solida (Busk)

Cellepora solida Busk, 1884 : 200, pl. 29, fig. 12. Waters, 1904 : 76, pl. 5, fig. 5.



Figs 19–22 Scanning electron micrographs of *Orthoporidra*; arrows indicate direction of colony growth; (19) *O. selida* (Busk) BMNH 1899.7.1.3525, S.W. Australia, tip of branch ×30; (20) *O. solida*, zooids with peristomial avicularia, central budding area (small arrows) ×50; (21) *O. compacta* (Waters) BMNH 1966.3.4.4, Halley Bay, Antarctica, zooids showing secondary frontal buds and interzooidal avicularium with ligulate bar ×50; (22) *O. compacta*, peristomial processes with avicularia, note thickness of calcification of frontal shield ×71.

SPECIMENS EXAMINED. BMNH, LECTOTYPE (chosen here), *Challenger* Stn 160, 4758m. 1899.7.1.3525, the specimen figured by Busk, 1884. Paralectotypes 1887.12.9.775–777; 1899.7.1.3526.

DESCRIPTION (Figs. 5, 14i, 19, 20). *Orthoporidra* with very large zooids, with numerous, scattered frontal septulae. Primary orifice and operculum curved proximally. Peristome not very prominent. Peristomial avicularia proximal and paired, lateral, raised on blunt mucros, mandibles rounded, rostra subtriangular. Interzooidal avicularia oval, large. Ovicells large, with small avicularia and scattered pores.

REMARKS. The colonies form branched cylindrical masses 5–10 mm in height. Secondary thickening is less developed than in *O. compacta*, and consists of numerous kenozooids as well as extrazooidal tissue. The avicularian processes are short and blunt, quite unlike those of *O. compacta.*

Busk (1884 : 200, pl. 29, fig. 12a) described the large interzooidal avicularia (as 'operculum' in the explanation of Plate 29), and Waters (1904, pl. 5, Fig. 5) also illustrated an operculum. The preparations in the BMNH show that the opercula are far larger than the dimensions indicated by Waters's figure.

Orthoporidra petiolata (Waters)

Cellepora petiolata Waters 1904 : 76 (*nom. nud.*); 1905 : 241, pl. 29, figs. 19, 20.
Catadysis petiolata: Hayward, 1980 : 714, Figs 5 E–H.

SPECIMENS EXAMINED. MM, T2–T6, Expedition Antarctique Belge. BMNH, Houtjes Bay, S. Africa, 1936.12.30.300c. Stn 346, Scottish National Antarctic Expedition, Burdwood Bank, 1981.3.1.12.

DESCRIPTION (Fig. 14h). Colony arising from a minute thickened base of kenozooids, encrusting erect bryozoa, 10–15 mm in height. Zooids with marginal and circum-oral septulae. Primary orifice and operculum with a small sinus. Suboral peristomial avicularium raised on long processes, mandible small, rounded or elongated and triangular. Ovicells small, prominent at first, with frontal pores and small avicularia. 14 tentacles (Waters).

REMARKS. Waters (1904) mentioned that a species which he proposed to name *'C. petiolata'* was similar in character to *O. compacta.* In his formal introduction (1905) he gave no further details, and figured only the operculum and mandibles. Waters's preparation (T5) shows an operculum with a small rounded sinus.

The generic assignment of *O. petiolata* is arbitrary. The orificial characters are similar to those of some species assigned here to *Turritigera* (e.g. *T. fenestella*), and to *Catadysis immersum* (see Hayward, 1980). The budding pattern of the zooids, and the distribution of the frontal septulae resemble those of *Orthoporidra compacta.*

Comparison of the Lekythoporidae with the genus *Orthoporidroides* Moyano

Frontally budded zooids with cryptocystidean frontal shields, which form massive or cylindrical, erect branches are typical of the Family Celleporinidae Harmer. Genera such as *Turbicellepora* (see Hayward, 1978) and *Celleporina* (see Harmer, 1957) also have oral avicularia derived from circum-oral frontal septulae, and often have elongated peristomes with terminal avicularia. Large, interzooidal (vicarious) frontally budded avicularia, and ovicells with porous frontal areas (tabulae) are also typical of these genera. The genera included in the Lekythoporidae are therefore distinguished from those in the Celleporinidae principally by their 'reversed' frontal budding pattern. The apparent close similarity between the Families is illustrated by *Orthoporidroides erectus* (Waters).

CELLEPORINIDAE Harmer

Celleporinidae Harmer, 1957 : 899.

ORTHOPORIDROIDES Moyano

Orthoporidroides Moyano, 1974 : 201. 1981.

TYPE SPECIES. *Cellepora armata* var. *erecta* Waters.

Orthoporidroides erectus (Waters)

Cellepora armata var. *erecta* Waters, 1888 : 36. pl. 3, figs 4, 41, 43.
Orthoporidroides erectus : Moyano, 1974 : 21, Figs. 6, 35–40.

SPECIMENS EXAMINED. BMNH, *Challenger* Stn 308, 320m, 1889.12.12.7. *Challenger* Stn 320. 1100m. 1888.3.14.3, 1899.7.1.3584, 3587, 3592, 3602, 3606; 1934.11.12.5. Shackleton-Rowett Exped., ?S. Orkney, 1923.12.1.39,48.

DESCRIPTION (Fig. 14j). Colonies erect, branching, arising from a small, encrusting base. Zooids budded frontally and distally, primary orifice with a shallow sinus directed towards the outside of the branch, operculum produced into a triangular sinus. Avicularia suboral, terminal on a long, proximally produced peristome, mandible acute. Ovicell hyperstomial, with a small, frontal slit.

REMARKS. Moyano (1974) has illustrated the morphology of *O. erectus* fully and compared it with that of *Turritigera stellata.* Moyano also noted similarities between *O. erectus* and *Cellepora petiolata* Waters (1905), see above. The opercula of *O. erectus* figured by Moyano resemble those illustrated by Waters, but differ slightly from those of the specimens from *Challenger* Stn 320, which are very variable (Fig. 14j). These specimens were not described by Busk (1884) or Waters (1888).

Discussion

Study of the relationships of the ovicell in the Lekythoporidae illustrates the importance of analysis of the astogenetic structure of colonies, as well as the ontogeny of their member zooids. It is interesting that since the ovicells of these genera were first described as 'proximal' in position, this monothetic 'character' has been accepted almost without question, and has even been modified (e.g. Harmer, 1957 : 884) in an attempt to include other taxa in the family, a frequent occurrence in bryozoan taxonomy (see Boardman *et al.,* 1969). The explanation of the unusual relationships of the ovicell has awaited first, the demonstration of frontal budding by Banta (1972) and second, the realisation that in both erect and rooted colonies, this type of astogeny may include reversal of zooidal orientation with respect to the direction of colony growth (see Cook & Lagaaij, 1976, and Cook & Chimonides, 1981).

The similarities in several characters among the genera assigned to the Lekythoporidae and Celleporinidae suggest a close relationship between the families.

It is possible that parallel complexes exist, each containing groups of species with totally different budding patterns, but with similar zooidal characters and even with similar resultant colony forms. *Orthoporidroides robusta* Moyano (1981 : 182, Figs 1–7), for example, resembles some other, unnamed Recent specimens from the Falkland Islands (BMNH, 1981.3.1.6,9,10) in illustrating how the type of budding pattern found in *O. erectus* may have been transformed into the type found in the Lekythoporidae. Colonies of both species are large, maximum height 50–60 mm, and profusely branched, with a range of zooid orientations. In *Orthoporidroides* sp. there are several sequential series of outwardly directed interzooidal, frontally budded zooids. The more centrally placed zooids of branches, which are those budded earlier in the astogenetic sequence, tend to have 'reversed' orientation of orifices, while the more numerous peripheral zooids have a 'normal' orientation. Some intermediate orientations, and ovicells in a 'proximal', lateral and distal topographical position occur in both *O. robusta* and the unnamed species. This differs from *O. robusta* in its orifice shape, which has a very long, narrow sinus, and the number of peripheral zooids in its branches.

At present it is difficult to determine whether or not astogeny and structure reflect closer genetic links than those of zooidal morphology. In order to trace possible changes in, for example, zooidal orientation and astogeny with time, a range of fossil specimens is necessary. Colonies of Lekythoporidae are robust enough to be preserved in fossil sediments; unfortunately only *L. hystrix* is unequivocally known to have a fossil record. Lack of records of other species, both in Recent and fossil deposits, is probably caused by difficulties of recognition, due to the small size of the colonies, and rapid thickening of extrazooidal calcification, which obscures the zooidal features. Recent species tend to inhabit the deeper shelf waters, and until more collections from these regions, particularly from high latitudes in the Southern hemisphere become available, detailed analysis of colonies is not possible.

Although the characters of the type-species of the five genera of Lekythoporidae are distinct, several of the other species described here show intermediate sets of correlations which make generic assignment somewhat arbitrary.

The 'easily recognised' character of the 'proximal ovicell' has to a great extent obscured analysis of other structures in the past. The fragmentary nature of most of the type material requires amplification by well preserved, complete colonies before the range of astogenetic, ontogenetic, polymorphic and microenvironmental variation of the taxa can be analysed and described.

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A new species of *Arthroleptis* (Anura: Ranidae) from the West Usambara Mountains, Tanzania

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The herpetology of the Usambara Mountains, Tanga Province, Tanzania is primarily based on the extensive collections made by Loveridge (Barbour & Loveridge, 1928). He concentrated his efforts on the more accessible eastern half of the Usambaras, especially around Amani (5°06′S: 38°37′E) at an elevation of around 923 m and appears to have been the only person who collected amphibians in the Mt. Lutindi outlier (Hindu of Moreau, 1935), the only part of East Usambaras that rises above 1219 m and has a patch of highland and cedar forest on its peak (1506 m) similar to that which, until comparatively recently, covered a vast area of West Usambaras (Moreau, 1935). Both the East and West Usambaras consist of high mountains with dramatically steep cliffs and ridges but the western peaks and plateaux are all above 1219 m, their highest ridges reach 2286 m and the rainfall is considerably less. The eastern and western divisions of the mountains are divided by the hot, dry trench-like Lwengera Valley which is nearly 914 m deep. The forests of the Highland Zone of the West Usambaras, as defined by Moreau (1935) in his excellent account of the topography, ecology and climate of these ancient mountains, remained virtually untouched by herpetologists until the last decade when collecting has been carried out by the writer and other zoologists, notably at ca 1530 m, 37·8 km NE Soni above Mombo at the Mazumbai Forest Reserve and tea plantation, 4°48′S: 38°29′E. This Forest Reserve consists of over 600 acres given to the University of Dar es Salaam by the owner of the tea plantation, Mr John Tanner. The most profitable collecting by the writer was done at 1530 m where an irrigation channel about 1·25 m wide follows the contour from a waterfall and river in forest passing through the forest to emerge in part of the plantation. The stream of approximately 140 mm depth had a slack to moderate current with a fine gravel and mud base. On its right bank it was overhung by forest trees while its left bank had a muddy track of sodden leaves plus debris backed by balsam and wild banana. The forest trees included *Ocotea usambarensis* and *Newtonia.* Average annual rainfall measured over a seven year period (1954/60), was 1041 mm. From a stone and debris in the stream and from the stream margin five *Arthroleptis* were obtained. These together with specimens found later by other collectors, at Mazumbai and additional localities in the West Usambaras between 1450 m and 2134 m, surpass in adult size all known species of *Arthroleptis.* In colour pattern and some proportions they resemble *A. affinis* Ahl, and to a much lesser extent *A. adolfifriederici* Nieden. A comparison of them with long series of *affinis* obtained mainly at the type locality, Amani in the East Usambaras, and with the type and paratype of Ruandan *adolfifriederici* suggests that an undescribed species of *Arthroleptis* exists in the West Usambara Mts.

The new species is named after Mr John Tanner in recognition of the generosity and hospitality afforded the collectors and other zoologists and his keen interest in the natural history of Mazumbai.

Abbreviations

BM(NH)	British Museum (Natural History), London
FMNH	Field Museum of Natural History, Chicago
R	Universitetets Zoologiske Museum, Copenhagen
ZMB	Zoologisches Museum der Humboldt-Universität Berlin

Bull. Br. Mus. nat. Hist. (Zool.) **45** (2): 77–84

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Arthroleptis tanneri sp. nov.

Arthroleptis adolfifriederici: Barbour & Loveridge 1928 (part)

HOLOTYPE. Adult female BM(NH) 1974.59, collected by A. G. C. Grandison and F. V. Slade at Mazumbai 4°48′S 38°29′E West Usambara Mountains, Tanzania, ca. 1530 m elevation, 1000 hrs, 8 October, 1973.

PARATYPES. Same locality data as for holotype: BM(NH) 1974.60 (stained and cleared preparation), BM(NH) 1974.61–63, 2245–2300 hrs., 8th October, 1973, BM(NH) 1974.200 16.30 hrs. 11th October 1973,m BM(NH) 1982.525–36, R 7731–35, R 7736–68, R 7797–98. Phillipshof 4°45′S 38°18′E (4 mls N of Lushoto), W. Usambara Mts: MCZ 13166. Shume-Magamba Forest Reserve, 4°40′S 38°15′E, W. Usambara Mts, 2134 m elevation, 11–16 February 1981: BM(NH) 1982.537–40. Balangai Reserve, 4°56′S 38°37′E, W. Usambara Mts, 1450 m elevation, May 1981: BM(NH) 1982.541.

DIAGNOSIS. A large *Arthroleptis* related to *A. adolfifriederici,* separable from that species and all other species of the genus by exceptional size (males 33·7±3·3: females 50·7 mm±4·9) and stout build. Further distinguished from the Usambara *A. affinis* by its shorter tibia, more widely set nares, slimmer, less pointed terminal phalanges, absence of supernumerary tubercles under the metatarsals, chin spinules but no denticulations along the second and third fingers in the adult male and by minor differences in the temporal colour pattern.

DESCRIPTION OF HOLOTYPE. Gravid female 54·0 mm SVL. Head slightly broader than long, its width 44% SVL. Length of snout from anterior border of eye to snout tip 35% of head width. Distance between the nares 11% of SVL. Canthus rostralis sharp, loreal region oblique, lips moderately flared. Interorbital region wider than upper eyelid, subequal to internarial distance. Tympanum clearly visible, the diameter of the tympanic annulus slightly greater than half the internarial distance. Snout rounded in dorsal view. Body stout. Terminal phalanges of fingers bluntly rounded, not or barely wider than distal joint, without circummarginal grooves. Toes long and slender, their terminal phalanges bluntly rounded with circummarginal grooves, the maximum width of the terminal phalanx of the 3rd toe about half the tympanic diameter and only 1/3 wider than the midpoint of the penultimate phalanx. No outer metatarsal tubercle or tarsal fold. Inner metatarsal tubercle broadly oval, its length 1/2 the distance from the tip of the 1st toe to the distal margin of the tubercle. Tibial length less than length of foot (measured from tip of 4th toe to proximal margin of inner metatarsal tubercle) 49% of SVL. No supernumerary tubercles proximal to basal subarticular tubercles of the toes. No toe web. Skin on the head and back smooth with a slight ridge extending along the canthus and lateral edge of the upper eyelid to form a curved dorsolateral line on the back.

COLOUR IN ALCOHOL. Dorsum mid brown with a darker rather obscure cruciform area extending from the interorbital area at the level of the middle of the eyelids to the middle of the shoulders, and bordered posteriorly by a broad pale chevron-shaped zone that is of the same intensity of brown as the top of the snout and upper eyelids. Behind the somewhat indistinct chevron is a darker area that reaches to the vent. The tip of the snout has a short light vertical streak. The lores are darker than the top of the snout and a prominent dark brown band passes from the posterior corner of the upper eyelid through the upper third of the tympanum and curves round the posterior rim of the tympanum ending at a point above the arm insertion. The under surfaces of the tarsus and metatarsus are dark brown, except for their outer edges which have a pale line from the heel along the external margin of the 5th toe to its tip. The legs and forelimbs are cross banded dark and lighter brown. The back of the thighs are mottled with pale grey. The middle of the belly is immaculate dirty white, the gular skin and chest pale fawn with creamy white mottling. The lower lip is medium brown, spotted or barred with white. Undersurfaces of the hind limbs dirty white with a faint greyish network. Undersurfaces of toes rather pale, the subarticular and metatarsal tubercles cream. Undersurfaces of hand uniform dirty cream.

HABITAT. The holotype and some of the British Museum paratypes were associated with *Rana angolensis* Bocage and *Phrynobatrachus krefftii* Boulenger. One adult female was on a stone jutting out of the stream, others in holes in rotten logs or under logs or on leaf litter, while the holotype and two other paratypes were among floating plant debris and twigs at the stream margin. The Copenhagen paratypes were reported as being on the forest floor about 1·6 km from water near to where the forest is replaced by heather on Mt. Sagara above Mazumbai.

COLOUR IN LIFE. The general dorsal colouration of the British Museum series was claret-brown with the chain of vertebral markings from the interorbital region to the lumbar region of a darker shade. The hands and feet were pinkish, especially their undersurfaces. Upper half of iris was pale gold.

VARIATION IN THE PARATYPES. There is a limited amount of variation in the distinctness of the dorsal pattern, the dark area over the occiput and the pale chevron immediately posterior to it being more clearly defined in younger individuals. Furthermore in the long series of smaller specimens (R 7736–68) some tend to have dark specks at the posterior margin of the chevron and small dark brown spots on flanks and temporal region. The cruciform area is replaced in some of the paratypes by a dark inverted triangular zone from the posterior limit of which two dark oblique bands extend towards the flanks. The undersurface of the head varies from grey mottled white to an almost uniform brown which in a sexually mature adult male has an even darker band laterally. The dorsal skin of the juvenile BM(NH) 1974.200 has small scattered warts.

SECONDARY SEXUAL CHARACTERS. As already indicated in the species diagnosis, male *tanneri* are smaller than females. Only four males are available and all have unpigmented testes. The smallest R7735 (30·0 mm SVL), is the only one that has spinules on the chin, and a dark brown almost black area along the lower jaw medial to the barred lip. No other secondary sexual differences are apparent. All the gravid females have large unpigmented eggs with a maximum diameter of 3·5 mm.

COMPARISON. Although *A. tanneri* attains a larger size than *A. affinis* Ahl, the taxon described from Amani, East Usambaras and reinstated by Skelton-Bougeois (1961), there is a strong superficial resemblance. However, statistically significant differences at the level P<0·001 using two sample t-test exist in the following percentage ratios of samples of the two species.

	A. tanneri		*A. affinis*	
	gravid ♀♀	♂♂♀♀, subadults	gravid ♀♀	♂♂♀♀, subadults
Head width	n 6	n 19	n 10	n 32
SVL	x̃ 44·17	x̃ 43·34	x̃ 42·0	x̃ 42·01
	S 1·17	S 1·86	S 1·56	S 1·29
Head width	n 6	n 19	n 11	n 32
Tibia length	x̃ 88·5	x̃ 84·31	x̃ 77·2	x̃ 75·36
	S 5·0	S 6·09	S 2·40	S 3·38
Tibia	n 6	n 19	n 13	n 32
SVL	x̃ 49·8	x̃ 51·83	x̃ 54·8	x̃ 55·78
	S 3·06	S 3·36	S 3·10	S 2·60
Internarial distance	n 6		n 11	
SVL	x̃ 11·15		x̃ 12·62	
	S 0·52		S 0·51	

No statistically significant differences in the percentage ratios of the internarial distance to SVL were found in samples of *tanneri* and *affinis* that included halfgrown individuals as well as adults of both sexes. Breeding males of *tanneri* and *affinis* may be distinguished by their different secondary sexual characters. None of the sexually mature male *affinis* has chin spinules but all have a row of denticulations along the inner border of the 2nd and 3rd fingers and the 3rd finger is elongated. Of the two males obtained by Loveridge at Phillipshof West Usambaras and identified by Barbour & Loveridge (1928) at *adolfifriederici* Nieden, the larger individual (37·4 mm SVL) MCZ 13166 has neither chin spinules nor denticulated fingers but agrees in proportions and in other characteristics with *tanneri* while the smaller specimen (29·1 mm SVL) MCZ 13167 is a typical *affinis* and has finger denticulations. Like all the males and females of *affinis* from the East Usambaras, both those from the Highland Zone (Mt. Lutindi) and from the Intermediate Forest of Amani, the Phillipshof example MCZ 13167 bears a prominent supernumerary tubercle under the distal portion of the 2nd and 3rd metatarsals and additional but smaller tubercles scattered over the sole of the foot. In some individuals of *affinis* a small tubercle is also present at the base of the first toe between the inner metatarsal tubercle and the subarticular tubercle (Fig. 2). Ahl (1939) in his type descriptions of *affinis* and of the junior synonym *A. schoenbecki,* both of which were obtained at Amani, mentions the supernumerary tubercles which bedeck the soles of the feet in the type specimens but makes no reference to the more distal tubercles under the 2nd and 3rd metatarsals. Examination of the type material in the present study has confirmed their presence.

Supernumerary tubercles under the metatarsals are absent from every individual of *tanneri,* as well as from the holotype and paratype of *A. adolfifriederici* from Rugege and Bugoya Forests Ruanda (Fig. 2). A third example also collected at Rugege and referred to *adolfifriederici* by Nieden (1912) also lacks these tubercles. However *adolfifriederici* differs from *A. tanneri* in its smaller size, the adult female holotype and paratype being 41·1 mm

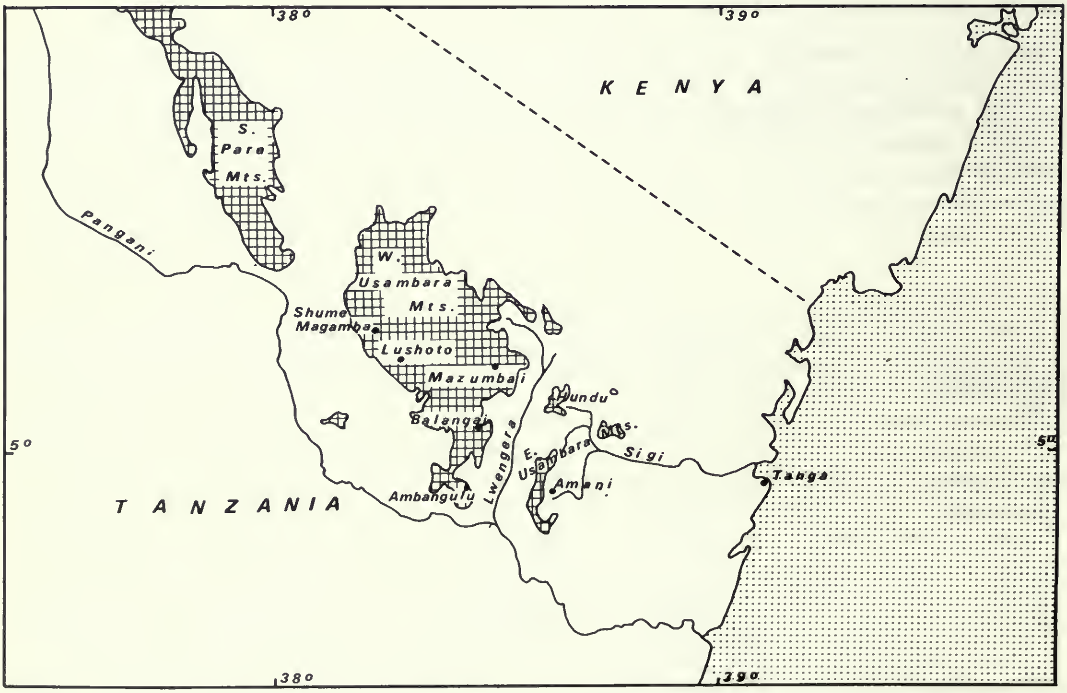

Fig. 1 The Usambara Mountains, NE Tanzania. Land over 1000 m is indicated by cross hatching.

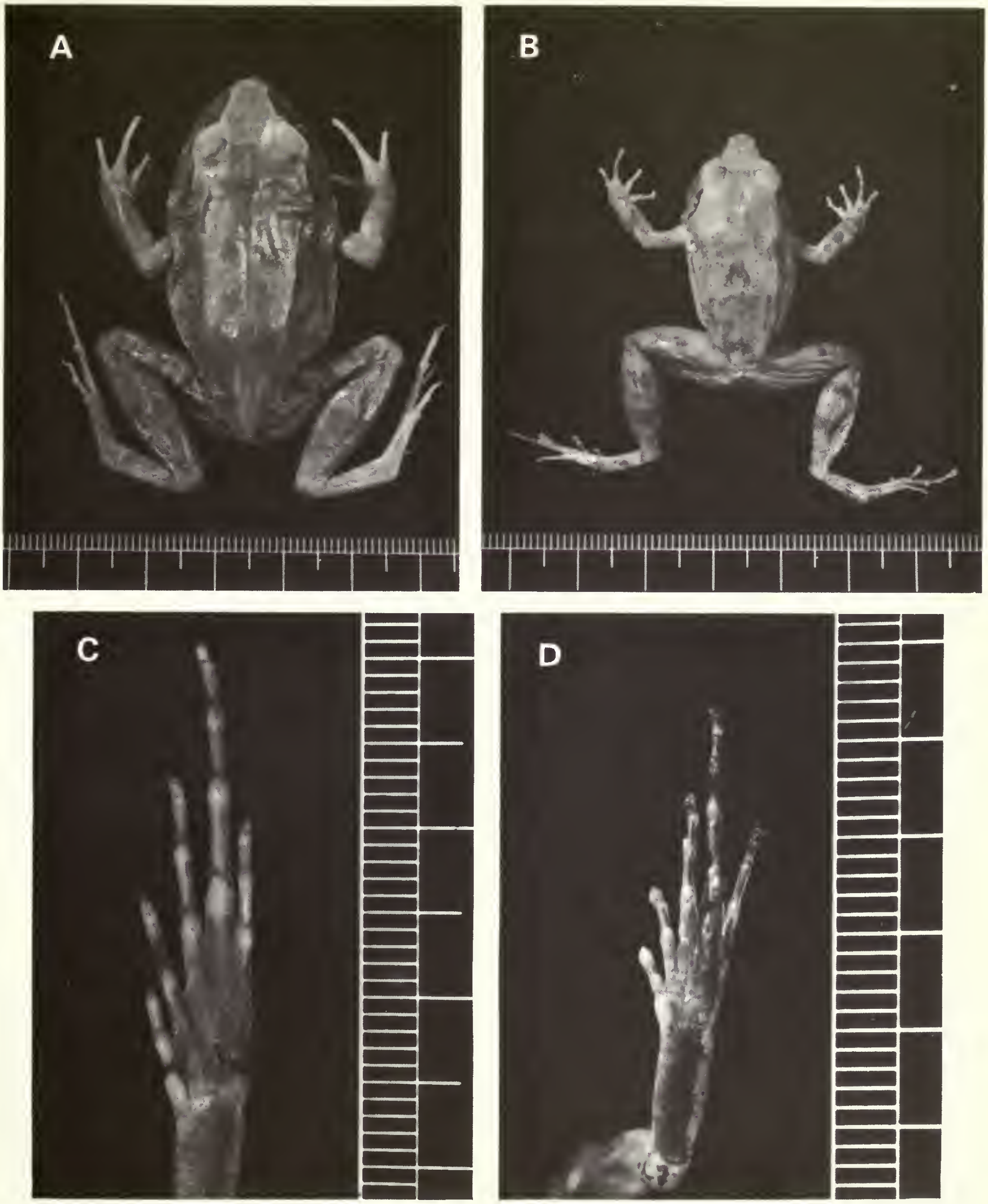

Fig. 2 Dorsal view and undersurface of the foot of: *Arthroleptis tanneri* sp. nov. (A & C); *Arthroleptis affinis* (B & D).

and 43·8 mm SVL, as well as in its marbled dorsal pattern (Nieden, 1912) and further differs from both *tanneri* and *affinis* in its much narrower head and shorter internarial distance and tibia. Percentage ratios in the holotype and paratype of *adolfifriederici* of head width/SVL are 35·0 and 33·1, of internarial distance/SVL 10·70 and 10·27, of head width/tibia length 61·0 and 55·34. *A. tanneri* seems to be further distinguished from either *adolfifriederici* or *affinis* by its terminal phalanges being bluntly rounded and barely wider than the distal joint. In the Ruanda *adolfifriederici* and in the East Usambara series of *affinis* they tend to be sharply pointed and are decidedly wider than the proximal phalanges and joints.

In colour pattern *tanneri* and *affinis* are rather similar but whereas in *tanneri* the ventral surfaces of the toes are cream, in *affinis* the phalanges and the soles of the feet are dark brown and the cream subarticular tubercles are in sharp contrast. Also in *affinis* the supratympanic stripe generally curves round the top of the tympanic annulus and does not pass across the tympanic membrane.

Osteology

The stained and cleared adult female paratype of *tanneri* was compared with a similarly prepared Amani adult of *affinis*. Osteological differences that are interpreted as being of taxonomic significance are limited to the skull, in particular the shape, extent of the sphenethmoid including the degree of its dorsal exposure, the medial separation of the nasals and the shape of the anterior borders of the frontoparietals.

In *tanneri* the sphenethmoid is a short squat bone, sharply concave posteriorly and with a straight anterior border that fails to reach the palatines except for their medial posterior tips. It has no dorsal exposure, being completely covered by the frontoparietals. The sphenethmoid in *affinis* not only projects much farther forward to extend well beyond the palatines and to the level of the anterior edges of the choanae, but its anterior and posterior borders are of a different shape from those of *tanneri*, being deeply convex and straight respectively. Furthermore the sphenethmoid has a crescentic dorsal exposure.

In both taxa the palatines are robust and contact the maxillae broadly but fail to reach the pterygoids.

Not only are the medial borders of the nasals more convex and wider apart in *affinis* but there is a greater separation between the nasals and the frontoparietals; moreover the anterior borders of the frontoparietals project forwards instead of as in *tanneri* being straight.

It is considered unlikely that these differences are attributable to individual variation in view of the author having discovered in an extensive analysis of bufonid skulls that there is virtually no intraspecific variation in adults in the shape and size of the sphenethmoid, palatines, nasals and frontoparietals.

Distribution of *A. tanneri* and its relationship with *A. affinis*

In the eastern half of the Usambara Mts *A. affinis* is known from Amani, 923 m, and from 1219 m on Mt. Lutindi (Hundu). In the neighbourhood of Amani during the dry season the writer found *affinis* to be abundant among leaf litter, in cracks in the impacted earth of road cuttings and in mounds of earth, sometimes in association with *Callulina kreffti* Nieden and *Nectophrynoides tornieri* Roux. Loveridge obtained 192 examples from leaf strewn paths at Amani (Barbour & Loveridge, 1928). At comparable elevations in the western half of the Usambaras no herpetological fieldwork has been undertaken below 1219 m and only one *Arthroleptis* has been taken at 1219 m, on the Ambangulu Estate, Korogwe District, 5°05′S, 38°26′E. The single individual, a juvenile of 20·0 mm displays features of both *tanneri* and *affinis*. It resembles *affinis* in having supernumerary tubercles under its metatarsals but its proportions correspond more closely to those of *tanneri*, its percentage ratios being Head width/SVL 45·0, Head width/Tibia 90·0 and Tibia/SVL 50·0. The existence of this aberrant individual raises the question of whether *tanneri* and *affinis* coexist at Ambangulu and whether the 'mixed' characters of this juvenile can be attributed to hybridisation. Further material from this and other localities at lower elevations in the West Usambara Mts is awaited with interest.

Evidence of sympatry of *A. tanneri* and *A. affinis* rests on the two adult males collected by

Loveridge in 1926 during ten days spent at Phillipshof in the West Usambaras. Barbour & Loveridge (1928) quote the elevation of Phillipshof as approximately 5500 ft (1676 m), which accords with information given to the author by the Royal Geographical Society based on the 1916 War Office maps of Tanganyika Territory and the Lushoto sheet 1 : 250 000 which place Phillipshof four miles north of Lushoto, 4°45′S 38°18′E, elevation 1524–1829 m. Barbour & Loveridge (1928) describe Phillipshof as 'rolling downs of grazing land, marshy swamps and slow-flowing streams in the bottoms, scattered patches of rain-forest on the uplands, with vast stretches of forest nearby on either side of the Malindi road'. According to Moreau's (1935) zonation of the Usambaras Phillipshof lies in the same Highland Zone as Mazumbai. It is not known whether the Phillipshof examples of *tanneri* and *affinis* were found in similar niches and closely associated with each other or whether they occupied quite different biotopes; no precise field data accompany the specimens. Except for the Phillipshof record of sympatry and the unique characters of the Ambangulu juvenile the available material points to *tanneri* and *affinis* being separated geographically and by altitude with *A. tanneri* confined to the West Usambara Mts in the Highland forest zone of Moreau (1935) and *A. affinis* occurring at the lower elevations of the Intermediate forest zone of the East Usambara Mts.

Additional material used in study

Arthroleptis adolfifriederici Nieden

Bugoya Forest, Ruanda: ZMB 21787 (Paratype).
Rugege Forest, Ruanda: ZMB 25287, FMNH 73836 (ZMB 21789) (Holotype).

Arthroleptis affinis Ahl

Amani 5°06′S 38°37′E, E. Usambara Mts, Tanzania 923 m: BM(NH) 1974.177 (stained and cleared preparation), BM(NH) 1974.170–176, BM(NH) 1974.178–185, BM(NH) 1974.186–195, MCZ 88131–278, MCZ 13153–60, FMNH 73836, ZMB 25289 (holotype of *A. schoenebecki* Ahl), ZMB 23093 (holotype of *A. affinis*), R 7797–98, R 77100.
Mt. Lutindi, E. Usambara Mts, Tanzania: MCZ 13161–65.
Phillipshof, W. Usambara Mts, Tanzania: MCZ 13167.

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The distribution, behavioural ecology and breeding strategy of the Pygmy Toad, *Mertensophryne micranotis* (Lov.)

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Introduction

Sexually mature males of the East African pygmy toad, *Mertensophryne micranotis* (Loveridge) have been reported as having series of small spines around the rim of the cloaca and at the entrance to the cloacal tube (Grandison, 1980). Development of these spines correlates with development of the cluster of heavily keratinised thumb spines and their function was interpreted as an adaptation for holding the vents of the male and female securely together during mating to ensure direct transfer of sperm to the small clutch of large eggs produced by the female. Spines in the area of an anuran's vent were first reported by Anderson (1871). He described a large zone of curved cornified papillae in *Rana gammi* Anderson, a species currently synonymised with *Rana (Paa) sikkimensis* Jerdon. Dubois (1976) figured the spines in *sikkimensis* and suggested that cornified spinules occur also in *Rana (Paa) delacouri* Angel. The life histories of neither of these Nepalese species is known.

In order to test the theory that had been postulated of internal fertilisation in *Mertensophryne micranotis* fieldwork and a captive breeding programme were recently undertaken in Kenya. New information on the species' occurrence in Kenya, its habits and breeding behaviour is presented here.

Range and ecological preferences

M. micranotis is known to occur in Tanzania, Zanzibar and Kenya. Few examples have been collected, perhaps because such a small-sized toad (sexual maturity is attained at 16 mm in males) is difficult to detect in leaf litter. Although the type and paratype found at Kilosa, Tanzania and a single individual from the Uluguru Mts. were said by Loveridge (1925) and Barbour & Loveridge (1928) respectively not to have been found in forest, elsewhere the species seems to be restricted to forest or recently cut down forest. In Kenya the species occurs both along the coast from Gede in the north (3°11′S: 40°1′E) to Shimoni in the south (4°38′S: 39°23′E), in the Shimba Hills National Park in the Coast Range (4°16′S: 39°22′E) and Mrima Hill (4°29′S: 39°16′E). Until comparatively recently the Coast Province of Kenya was a near continuous forested belt overlying the approximately three kilometre wide Pleistocene coral reef and the Pliocene and Pleistocene sandy soils adjacent to it farther inland. Today little true forest remains in the Coast Province and very few remnants extend to more than 50 acres. Agriculture, notably plantations of sugar, coconut, cashew nut, maize and sisal combined with the rapid growth of Kenya's tourist industry have taken their toll of the coastal forests. Two of the small remaining pockets are contained in the

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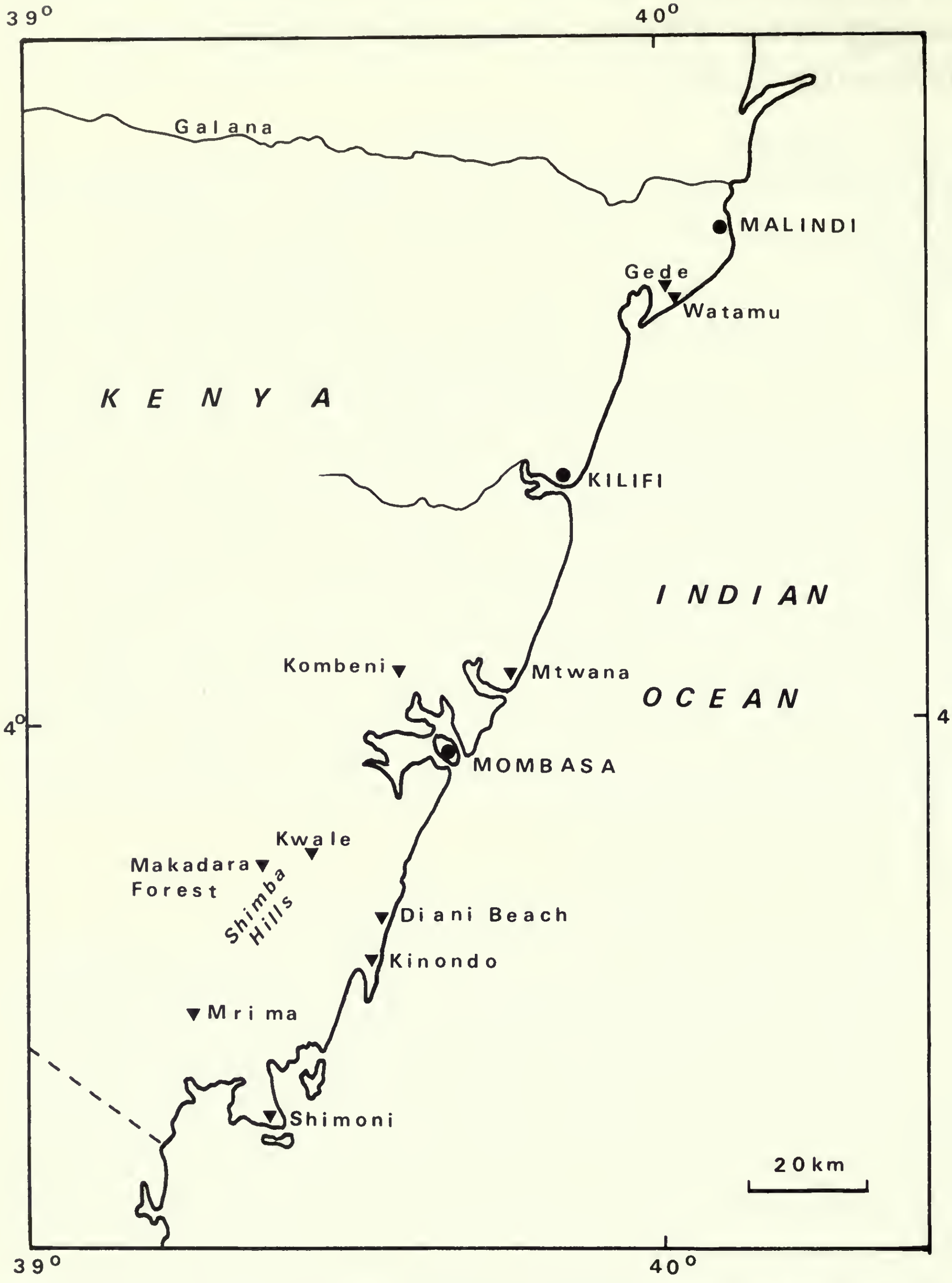
3 9°
4 0°
Galana
MALINDI
Gede
Watamu
K E N Y A
KILIFI
I N D I A N
Kombeni
Mtwana
O C E A N
4°
4°
MOMBASA
Kwale
Makadara
Forest
Shimba
Hills
Diani Beach
Kinondo
Mrima
Shimoni
2 0 km
3 9°
4 0°

Fig. 1 Known distribution of *Mertensophryne micranotis* (Loveridge) in Kenya. Records indicated by an inverted triangle.

National Monuments of Gede and Mtwana, in which are preserved the ruins of thirteenth century Arab–African towns. Diani forest (sometimes also referred to as Jadini forest) consists of 50 acres of largely untouched forest similar in composition to Gede forest; it is privately owned. Other small forest relics encircle cleared areas that until the nineteenth century were settlements, each housing up to 2000 of the Mijikenda peoples but which today contain only a few houses occupied by elders of the clans and graves of their ancestors. Most of these kayas, as these sacred villages are called, were situated along the ridge of the Coast Range from the Shimba Hills northwards to Kilifi and at vantage points to resist incursions from the north by the Galla farmers. By the seventeenth century the most southerly of the Mijikenda, the Digo, vacated their Shimba kaya and established minor kayas along the coastal plain (Spear, 1978). At one such sub-kaya, Kinondo, and at the Kombeni kaya *M. micranotis* has been found. On account of their religious significance and present day use for rituals and processions the kaya forests are provided with a measure of protection which may safeguard their populations of *micranotis*.

In the southern extremity of the Coast Province two densely forested hills, Jombo and Mrima, jut up spectacularly from the surrounding flat plains (Britton *et al.,* 1980). No herpetological survey has apparently ever been made of Jombo (476 m) but the senior author made two short visits to nearby Mrima which rises to 299 m. The very deeply weathered volcanic plug of Mrima has been prospected since the early 1950s for its rich deposits of manganese and niobium. Its rocks weather extremely rapidly and up to 236 m of terra rosa cover the carbonatite plug. It is the weathered material that has been mined and the abandoned and completely unprotected mineshafts are a serious hazard to contend with when scouring the upper reaches of the forest for the anuran denizens of the leaf litter. A circular, flat-topped pile of moist leaves which contained duiker droppings and may have been a communal duiker latrine on to which some animals, perhaps ants, had piled leaves and other debris yielded juvenile *M. micranotis.* The pile was on a trail and was the only damp spot found; no rain appeared to have fallen for some considerable time and no water-filled treeholes were evident. On the bank of a path and among small pieces of weathered carbonatite and terra rosa and harmonising perfectly in colouration another juvenile *micranotis* was obtained. In these forests there are no surface ponds or streams and even after heavy and prolonged rain the water probably rapidly disappears through the red earth and litter that overly and form pockets in the labyrinth of holes in the coral rag of the narrow coastal strip. On the sandy soils farther inland the rains likewise drain rapidly. The only standing water that becomes available with the highly seasonal rains are ephemeral reservoirs in treeholes formed by broken off limbs, in fissures in tree buttresses and in live and fallen tree trunks, as well as in abandoned shells of the large land snail, *Achatina,* and in the occasional discarded can on the forest floor. Consequently the only anurans that can survive in such forests need to have a highly specialised breeding strategy, such as direct development that completely omits the larval stage or one that produces a terrestrial larva, or need to be opportunistic breeders capable of taking advantage of the seasonal water pockets for egg laying sites. As the water holes are small and subject to rapid desiccation small clutches capable of an accelerated rate of development would be to the species' advantage.

The searches made of the forest litter, of trees and shrubs in these Kenyan forests have revealed only three species of Anura, two of them arthroleptines a group known to develop directly from eggs laid in underground chambers to fully transformed miniatures of the adult frogs. The third, *Mertensophryne micranotis,* has been reported as breeding in water-filled treeholes and land snail shells and has an unusual-shaped tadpole with an angled head that is surrounded by a raised ring of tissue (Grandison, 1980). The anuran composition of a waterless forest in SE Tanzania is recorded by Loveridge (1942). The area is Nchingida 10°8´S, 39°12´E on the Rondo Plateau which is the type locality of *Mertensophryne micranotis rondoensis* (Loveridge), a form that Loveridge distinguished from the nominate on its less heavily pigmented throat. Loveridge (1944) described the Rondo Plateau as waterless where even the heaviest rainstorms drain rapidly through the sandy soils. In addition to the *M. m.*

rondoensis he recorded (1942, 1944) four other species of Anura—two arthroleptines and two microhylids, *Breviceps mossambicus* Peters and *Spelaeophryne methneri* Ahl. While the life history of *Breviceps* is known to be entirely independent of water (Wager, 1965), very large eggs being laid in burrows often far from water and the tadpole stage passed within the egg capsule, no aspect of the breeding cycle of *Spelaeophryne* has been recorded. The right ovary removed from an adult female *S. methneri* in the BM collections contains 18 large ova, average diameter 2 mm, and a few much smaller ova: all are unpigmented. Such a small clutch of unpigmented eggs suggests a specialised reproductive mode that has freed the species from an aquatic environment, although since the species lacks any obvious means of burrowing into the litter, unlike *Arthroleptis stenodactylus* Pfeffer and *Breviceps* with their well developed shovel-shaped metatarsal tubercles, it seems unlikely that *Spelaeophryne* is a burrowing breeder. Perhaps like *Nectophrynoides malcolmi* Grandison (1978) it has a terrestrial tadpole with a vascularised tail that serves as a respiratory organ, but perhaps like *Mertensophryne micranotis* it depends on waterfilled holes in which to lay its small complement of eggs.

The senior author's field study was conducted during the month of May. Mean monthly rainfall records had suggested that this period would be the most likely to coincide with the long rains and consequently produce water-filled breeding sites and the likelihood of witnessing breeding behaviour in the species. However the rains were capricious in May 1981 and at Diani Beach in the southern coastal belt only 19 cm fell during the entire month and for half the period there was no rain or only a few drops (C. Harcourt, pers. comm.); as a result the number of water-filled treeholes and land snail shells was exceedingly small and no mating pairs were found. The standing water in all treeholes found was siphoned and checked for the presence of anuran eggs and tadpoles but only one sample contained *micranotis* tadpoles; it was in one of three holes in the buttress formation of a tree that branched near its base into three trunks and was the only one obscured by a green leafy liana which partly shaded it from the sun. The diameter of the tree trunk at the level of the hole was 54 cm. The other two waterfilled holes in the same tree were at a similar height from the forest floor and although their sizes fall within the range of variation of other oviposition sites for *micranotis* the holes contained only insect larvae (Table 1). All the tadpoles, in excess of 45, had developed limbs but still had larval mouthparts. The pH of the water was not taken and the identity of the tree is not known.

The mammalogist, Dr G. Rathbun, reports (pers. comm.) that while studying elephant shrews and cutting forest trails at Gede he was attracted by a faint squeak to a hole in a tree

Table 1 Records of water-filled treeholes occupied by *Mertensophryne micranotis*. From data supplied by G. Rathbun (†) and L. P. Lounibos (*)

Location	Date	Height from forest floor (cm)	Diameter (cm)	Depth (cm)	Volume of water (cc)	Larvae (L) or Toads (T)
† Gede	18.v.71	150·0		10·16	Full	T (♂ and ♀)
* Kombeni	16.v.75				700	L
	16.v.75				230	L
	24.iv.76				90	L
	24.iv.76	30·48	3·8×5·1	5·08	55	L
	27.iv.76	101·60	3·8×7·6	7·62	20	L
	7.v.77				60	T (in amplexus)
* Makadara	11.iv.76	17·78	2·5×2·5	6·35	70	L
	11.iv.76	96·52	2·5×2·5	6·35	25	L
	19.iv.76	121·92	3·8×3·8	7·37	45	L
Shimoni	12.v.81	20·32	2·5×3·8	10·16	Full	L

7·6 cm diameter which he tentatively identified as *Lecaniodiscus fraxinifolius.* The hole was in a stump formed by a fallen limb 1·5 m from the forest floor. It contained a pair of sexually mature *M. micranotis* which suggests that the hole had been selected as a potential breeding site. Dr L. P. Lounibos (pers. comm.) provides the only other known records of the occurrence of *micranotis* in water-filled treeholes. His records and details of the Gede and Shimoni treeholes are given in Table 1. Dr Lounibos' observations were made in the course of his research into mosquito habitat segregation in Makadara Forest Shimba Hills and Kombeni Forest, Rabai Location (3°55′S: 39°34′E). Samples of his Makadara Forest tadpoles and adults were identified by A. McKay, National Museums, Kenya and the identity of a sexually mature male obtained at Kinondo Forest was confirmed by the senior author. It is assumed that his Kombeni tadpoles and toads were also correctly identified. Lounibos (1981) should be consulted for rainfall records and seasonality of water in treeholes in his study areas.

Movements, colour change and territorial behaviour

Skulking movements and exceptionally effective camouflage are striking features of *M. micranotis.* Adults and subadults when disturbed on the forest floor tend to remain motionless or to very slowly back under a dead leaf or twig or disappear down a hole. A gravid female unearthed from loose soil at the base of a tree flattened its body and remained inert for some time after capture and to the extent that it resembled a dead leaf.

The disruptive dorsal colour pattern of shades of brown closely matches the leaf litter in which *micranotis* is usually found and makes the animal exceedingly difficult to detect. The darkest areas of the body are invariably the lateral band and the interocular bar. A pale hair-like vertebral line of variable length, but usually extending from behind the eyes to the sacrum is present in most specimens. It is sometimes flanked by an irregular dark brown band that divides in the sacral region to form a large ring enclosing a pale zone which extends posteriorly to a brilliant white supra-anal triangle. This white triangle is characteristic of the species. The dark vertebral band and ring are separated from the even darker lateral band by a broad lighter area which is particularly subject to variation in colour according to the animal's background. For instance, in an adult male transported on white plastic foam this dorsolateral area was a very pale grey but after a day spent on dead leaves, twigs and bark the entire dorsum changed to dark brown, while two days later the pale grey areas changed to khaki. Both in its dark and khaki phases the toad was barely discernible among the litter. Recently transformed juveniles and halfgrown individuals are usually black when they emerge from their hiding places but may acquire a greenish-brown tinge when more active. Ventrally, both adults and young have prominent dark blotches on a white background. Males tend to have a brighter, more contrasting colour pattern than females. Observations on captive individuals suggest that the species is diurnal and particularly active in the morning, also that it is territorial, with individuals having their own burrows in the leaf litter. In the wild it is likely that members of the species occurring in forest overlying coral rag will use as retreats the abundant holes in the coral as well as burrows in soil and leaf litter. After active foraging the toads usually back down into their burrows. Adults are more secretive than juveniles and were not seen to make their presence obvious by hopping or other rapid movements; their movements were exceedingly slow, laborious and consisted of usually no more than five steps at a time followed by a long pause. On the other hand, juveniles tended to scramble and hop but such activity was interspersed with long periods of immobility.

The junior author noticed the species' propensity while in captivity to climb. Day old toadlets climbed with apparent ease the glass sides of a casserole in which they were reared. Generally they moved hand over hand with the body raised but when climbing clean glass they lowered their bodies. Adults not only readily climbed the plants in the terrarium, occasionally roosting on leaves and crawling along narrow stems but they persistently climbed the glass sides of the rectangular tank usually by straddling a corner of the terrarium and bracing their limbs. As they climbed the glass it was noticed that they left behind a trail of liquid and that the posterior part of the toad's abdomen was flattened on the substrate. It is believed that the liquid is expelled from the toad's cloaca and that the surface tension set up facilitates progression over a smooth surface. By developing a technique that allows a short and spindly legged species to climb smooth vertical surfaces the availability and variety of treehole oviposition sites may also be increased thus enhancing the chances of survival.

Captive breeding programme

One subadult and eleven juveniles collected between 29 June and 11 July 1981 were reared in captivity to sexual maturity. They were collected from an area of less than an acre in the vicinity of the junior author's house at Watamu. The area once covered by primary forest and an extension of the Gede Forest was cleared of all but the large trees for house building in 1980. The toads were found on and among the leaf litter overlying coral rag in or at the edge of a surveyor's cut line as well as in a large termite-ridden rotten log in the undergrowth.

The terrarium consisted of a glass tank $40 \times 28 \times 22{\cdot}5$ cm furnished with a 2–5 cm layer of leaf litter and sand, growing plants and logs. A coconut shell with a little rain water and a plastic jar 12 cm deep and a 6 cm diameter, filled with rainwater and tilted at an angle of 45° against a twisted root provided potential oviposition sites. The root acted as a climbing frame and provided numerous hiding places. A wooden ramp in the jar of water formed an exit.

By the 22 October, five days after the rains had started the day temperature exceeded 30°C and night time temperature 25°C and there was high humidity, the first batch of eggs was laid but neither mating nor egg laying was witnessed. Several toads appeared gravid.

The following accounts are condensed from the detailed notes made by the junior author on her observations on the mating behaviour of her captive specimens.

Courtship

It remains uncertain whether females approach individual males and what signals are used to initiate courtship because pairs were already in amplexus on each occasion when observations were begun. However it was noticed that the soft chirp of a male in amplexus prompted three other males that had been chasing each other around in the water container to call and mount each other indiscriminately and their calls appeared to induce two females to move in the direction of their calls but stop and wander off when the calling ceased. The behaviour of the three males in the jar suggests that the normal calling-station may be a water-filled container and that the receptive female moves in that direction when stimulated by the advertisement call. However the mating behaviour of only six pairs has been observed and while one pair mated in water the other pairs mated mostly out of water. Visual as well as auditory cues may contribute to mate selection in *M. micranotis* for it was noted that the three calling males in the water jar were of a brighter colour and more contrasting pattern than the amplectic male which was very dark coloured.

Amplexus and fertilisation

The mating of one pair, which spanned a period of over eight hours, is described in detail. When the male first mounted the female, their eyes were in the same vertical plane while his hind legs trailed on the ground. The amplectic position was axillary. As he drew up his legs he stimulated the female's sacroiliacal region by drumming it with his long fourth toe then placed his feet over her tibiotarsal joints. Half an hour later he uttered an almost inaudible rapid ticking sound which the female answered with a soft chirp. The pair were clamped closely to each other from snout to vent but although their white supraanal patches were vertically in line a distance of about 2 mm separated them. After an interval of about a few minutes the female alternately inflated and deflated her body, as if sighing, while his feet were placed on her flanks. As her body deflated at 30 second intervals the male exerted a downward squeeze with his cloacal region. Despite the female moving away and trying to dislodge the male by scratching him first with her hind leg then with a front leg, the male remained firmly attached, although at one point he was shifted sideways as she forced her way under a piece of bark. Mating movements were discontinued while the female fed on white ants but were resumed approximately two hours after observations on the amplectic pair were begun. The male resumed tactile stimulation of the female by drumming his fourth toe. His heels which were then placed on either side of and slightly above her white supraanal patch seemed to channel the drop of clear liquid that trickled from his cloaca down to hers where it appeared to be absorbed. As the female adopted a more upright stance the male moved farther back and lower down and his mating movements became more forceful. As he engaged in a series of thrusts his white supraanal patch was seen to curl inwards towards that of the female. During the ensuing two hours mating movements continued intermittently, with a rest period while the female, still with male attached, moved to a hiding place in the litter but when the amplectic male produced a rapid, very faint ticking sound another male called from 25 cm away in the water jar; the vocalisation elicited a marked increase in activity by all the other males in the terrarium which chased and mounted each other indiscriminately while their calls became louder until each call sounded like a ten note chirp which could be heard 2·5 m away. Several females were active on the floor of the terrarium but although one of the calling males attempted to mount a female it did not persist when the female moved away. When the amplectic pair emerged from the hiding place more vigorous mating movements occurred, despite the female's attempts on two occasions to dislodge the male, and he thrust twice each time the female deflated her body. Although both sexes were visibly vibrating no call from the female was audible but the male emitted a ticking sound. During the next hour sporadic mating movements occurred but his vent was above hers and although the pair entered the coconut shell partly filled with water and moved round the slope in a clockwise direction only her foot entered the water and the pair climbed out of the shell. The female again tried to dislodge the male while she ate insects. Observation was discontinued for ten minutes during which time the pair disappeared.

In five other pairs in which mating was witnessed the duration of amplexus varied from five and a half hours to ten hours. It was noticed that the male's grip on the female's vent is so tight that his vent drags upwards the skin surrounding her vent. One pair found in the water jar in the 'normal' amplectic position were joined by a second male which clung to the female's axillae in an inverted, belly to belly position. Both males engaged in mating movements but two hours later when the dorsal male had disappeared the protruding cloacal region of the underslung male was seen to curl upwards to contact that of the female and the moisture he expelled from his vent as he thrust appeared to immediately be absorbed by the female. Belly to belly amplexus is known to occur also in the internally fertilised Ethiopian bufonid, *Nectophrynoides malcolmi* Grandison (Grandison, 1978 and Wake, 1980).

Although clutches of eggs were later found in the jar of water in the terrarium, egg laying by mated females had not been witnessed and because males were present the possibility of the eggs having been externally fertilised could not be ruled out. So on the next occasion when a pair began to mate they were removed to another terrarium containing a water bowl of similar capacity and quantity of water. When mating was completed and the male had dismounted he was removed and returned to his original terrarium. Mating had taken place in water. Six hours after mating the female, still in the water, began laying eggs, two strings emerging together. Three and a half hours from the start of egg laying and at 2300 hours oviposition had not been completed, but the following morning two eggs strings containing a total of 22 eggs were found attached to the rim of the jar. The female had returned to the floor of the terrarium. The eggs proved to be fertile and they developed at a similar rate to those in previous clutches. Each of the six eggs in one string that was severed and preserved within forty minutes of being laid was found to be at the late cleavage stage of development, but eggs from another clutch where the time of laying was unknown were at early to late gastrula. The number of eggs in five clutches were 17, 19, 22, 32, 32.

The aforegoing description emphasises the close contact of the cloacae during mating in *Mertensophryne micranotis* and the tenacious grip that the male exerts on the female's vent while he engages in downward thrusts and his feet are placed on each side of the female's vent. While it can be assumed that the male's cloacal spines play a significant part in the coupling and that internal fertilisation of the eggs takes place it is still not known whether the spines interlock in the furrows of the female's vent.

Function of the tadpole's head 'crown'

Broadley (in Channing, 1978) suggested that the function of the head 'crown' in tadpoles of *Stephopaedes anotis* (Boulenger) might be to exclude from the eyes and nostrils scum accumulating on the water surface. The angled head and ring of raised tissue ('crown') of the *M. micranotis* tadpole is closely similar to that of *S. anotis* (Grandison, 1980) but observations on tadpoles of *M. micranotis* in the wild and in captivity suggest that the angled head with the raised ring of tissue surrounding a saucer-like depression in which lie the eyes and nostrils is a simple adaptation for suspending the tadpole at the meniscus, where the highest concentration of oxygenated water is available in the small pocket of stagnant water that is selected as a breeding site. With the 'crown' breaking the water surface the tadpole has access to oxygen, both during its gill breathing stages and later when it has acquired lungs, at the same time maintaining itself in a tail-down position with the minimum expenditure of energy. In the field study it was noticed that each time the sun struck the water surface of the treehole the tadpoles tended to rise quickly and suspend themselves at the meniscus, particularly around the rim of the hole so that their angled heads were parallel to the contour of the meniscus whilst the body and tail of the tadpole hung down vertically. In such a position the ventral mouthparts had access to the algal growth lining the rim of the cavity. When the head 'crown', which is at an angle of 45° to the body and tail, breaks the surface tension at or near the centre of the hole where the meniscus is virtually horizontal the body and tail of the tadpole are suspended parallel to the angle of the head.

Diet

The contents of the stomachs of three subadults that were known to have been preserved immediately after capture were analysed. Ants constituted the major food element but mites were found to have been almost equally favoured, particularly *Linopodes* (Eupodidae). Although nine other genera of mites were present only one or two examples of each were identified (*Eupelops, Trachygalumna, Pilizetes, Liodes, Eremaezetes, Scapheremaeus, Bdella* and *Spinibdella*). Beetles and thrips of kinds typical of the litter/subcortical layer were also represented in the analysis, as well as Collembola (*Symphypleona*) and the macerated remains of spiders and fly larvae. The only trace of termites was a crumpled set of wings of Termitidae. In captivity the toads thrived on a diet of small white ants, termites and aphids.

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Additional notes on bariliine cyprinid fishes

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This addendum serves to correct and amplify statements and observations published in an earlier study on the anatomy, phylogeny and classification of bariliine cyprinid fishes (Howes, 1980).

The generic status of *Barilius lujae* Boulenger, 1909

In the synoptic account of *Barilius* species given in Howes (1980), *Barilius lujae* Blgr, 1909 was omitted. Examination of syntypes (BMNH 1908.11.26 : 8; 1909.4.26 : 18), together with a series of more recently collected specimens (BMNH 1975.6.20 : 429–438; 1976.6.20 : 407–413, including alizarin preparations), makes it clear that the species *lujae* should be assigned to the genus *Leptocypris.*

Synapomorphies characterising *Leptocypris* (modified from Howes, 1980) are: shallow lower jaw; truncated lateral ethmoid; absence of, or reduced *intermandibularis* muscle; absence of, or few gill-rakers; elongated pectoral and pelvic axial scales, and overlap of the antero-dorsal portion of the 2nd infraorbital by the posterior border of the 1st. The species *lujae* has all these characters and, in addition, a type of ethmoid architecture which supports the hypothesis that *Leptocypris* and *Engraulicypris* are closely related genera (Howes, 1980 : 182).

In *Leptocypris lujae* the medial ethmoid notch is horseshoe-shaped as in *Engraulicypris sardella* (cf. Fig. 1 here with fig. 9 in Howes, 1980). In *Engraulicypris* the ethmoid indentation coincides with a foramen in the underlying vomer, whereas in *L. lujae* the indentation is floored partly by the ethmoid cartilage and partly by the vomer.

Compared with other species of *Leptocypris, L. lujae* is longer-jawed, the posterior tip of the maxilla extending to, or beyond, the posterior rim of the orbit; there is also a lower jaw symphysial process. As in *L. niloticus* and *L. weynsii, L. lujae* has a non-papillate maxillary valve. There is some variability in the length of the pelvic axial scale, it varies between 42%–50% of the pelvic fin length. However, this appears to be positively correlated with the length of the fish and it is noted that in *L. niloticus* the pelvic scale is not developed to its maximum length (25% of the pelvic fin length) until the fish is over 35 mm SL.

In the length of the jaws and the morphology of the ethmoid region, *L. lujae* appears to be the most derived species. The species of *Leptocypris* may be identified by the following key:

1.	Gill-rakers on first ceratobranchial absent; branched anal fin rays 8–9	***L. modestus***
	Gillrakers on first ceratobranchial 2–3; branched anal fin rays 11–15	2
2.	Branched anal fin rays 11–12	***L. niloticus***
	Branched anal fin rays 14–15	3
3	Posterior tip of maxilla extending to centre of eye; lateral line scales 44–45	***L. weynsii***
	Posterior tip of maxilla extending to, or beyond posterior border of the eye; lateral line scales 38–40	***L. lujae***

Attention is drawn to *'Barilius' guineensis* Daget, 1962, which appears, from its gross morphology, to belong to *Leptocypris* (see Howes, 1980 : 191). It differs from other species, however, in (according to Daget, 1962) having a total of 8 gill-rakers on the first arch.

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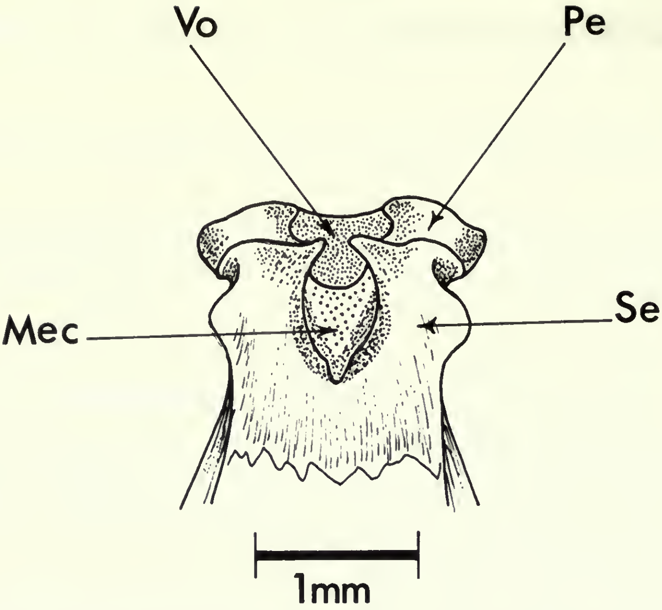

Fig. 1 *Leptocypris lujae*; dorsal view of ethmovomerine region of the neurocranium. Mec = mesethmoid cartilage, Pe = preethmoid, Se = supraethmoid, Vo = vomer.

Comments on south-east Asian *Barilius* species

When offering a revised concept of *Barilius* (Howes, 1980), based on the type species of the genus *B. barila,* few of the south-east Asian species had been examined and their generic attribution remained doubtful. Of those species in this category (Howes, 1980 : 190) the following have now been examined: *B. bernatziki* Koumans, 1937 (Holotype, Basle Museum, NHMB 5155, 77 mm SL); *B. huahinensis* Fowler, 1934 (USNM 103104, 52 & 66 mm SL); *B. infrafasciatus* Fowler, 1934 (USNM 107910, 65–75 mm SL); *B. koratensis* Smith, 1931 (Holotype, USMN 90298 47·3 mm SL); *B. nanensis* Smith, 1945 (Paratypes USNM 107939, 107940, 119474–119476, 53–64 mm SL); *B. pulchellus* Smith, 1931 (Paratypes USNM 90299, 51 & 53 mm SL; USNM 107967, 39·5–69·5 mm SL).

Osteologically and meristically, these species are intermediate between the generic subgroups (i) and (ii) previously postulated (Howes, 1980 : 180), possessing characters of both groups. This suggests that those characters used in defining the two groups are a mixture of plesio- and apomorphies.

In the south-east Asian species, and noticeably in *B. pulchellus,* the ethmoid bloc is somewhat flattened with the vomer extending anteriorly to the mesethmoid. The lateral edges of the supraethmoid are slightly raised to produce a shallow channel. The maxilla has a tall mid-lateral (palatine) ascending process and the palatine is broad anteriorly, slightly overlapping the maxilla and supporting the base of the anterior barbel. Rows of tubercles appear on the lower jaw and infraorbitals. These characters are shared with the Indian species, *B. gatensis* and *B. bendelisis,* and those species referred to group (ii) by Howes (1980 : 190). The morphology of the ethmo-vomerine region, lateral extension of the palatine, and the pattern of tubercle development on the lower jaw appear synapomorphic for this group of species. As such, the concept of *Barilius* presented previously (Howes, 1980) is shown to be a paraphyletic one; see below, p. 99.

The taxonomy of the south-east Asian species is in an unsatisfactory state. Smith (1945) separates *B. nanensis* and *B. huahinensis* on the differences in lateral line scale counts, dorsal fin position, and length of the anterior (rostral) barbel. However, there appears to be variability and overlap in all these characters, although the differences in body markings between the two species quoted by Smith (1945 : 156–157) are consistent. In *B. nanensis* there are 7–8 gill-rakers on the 1st ceratobranchial cf. 9–10 in *B. huahinensis.*

Barilius pulchellus Smith, 1931 is a distinctive species characterised by a large pectoral axial fin lobe, 3–6 minute, spiny gill-rakers on the 1st ceratobranchial, and a black dorsal fin membrane. Specimens identified as *B. infrafasciatus* Fowler, 1934 (type not seen) are similar in virtually every respect to *B. pulchellus* apart from the length of the pelvic axial scale which is 50% of the pelvic fin length cf. 25% in *B. pulchellus.*

Smith (1931) described *Barilius koratensis* as without barbels. My examination of the unique holotype reveals both anterior and posterior barbels. Smith described only two vertical bars, above the pectoral and below the dorsal fin, but there is also a dark patch above the last ray of the anal fin. In other meristic and morphometric characters *B. koratensis* resembles *B. nanensis*; these taxa may well be only representatives of different populations of one species.

Barilius bernatziki Koumans, 1937 has 30–31 lateral line scales, the least number of all the south-east Asian species. In its markings (7 dark vertical bands and basal caudal spot), large pectoral axial lobe, and narrow cranium, *B. bernatziki* most closely resembles the Indian species, *B. gatensis.*

The phyletic position of *Zacco*

Zacco was excluded from the bariliine group by Howes (1980) on the grounds that it lacked a posttemporal–subtemporal connection. Fink & Fink (1981) claim this feature is present, and an examination of additional material leads me to agree with them. If *Zacco* is included within the bariliine assemblage, characters which were previously regarded as examples of homoplasy (peculiar morphology of the anal fin, ventral prolongation of the caudal peduncle and colour pattern), must now be viewed as synapomorphies.

Zacco must be regarded as the sister taxon to *Opsariichthys* and because of its less derived cranial architecture and relatively unmodified lower jaw, it is the plesiomorph partner. Inclusion of *Zacco* within the bariliine group does not alter the group's distribution mapped in Howes (1980, fig. 47).

Monophyly of the bariliine group

According to Fink & Fink (1981) a number of characters used by Howes (1980) to define the bariliine group are plesiomorphic. Of these they list the ventrally open posterior myodome; trigeminal foramen entirely within the prootic; lateral hyomandibular flange; frontal fossa; lateral temporal foramen, and the metapterygoid postero-dorsal process. They also believe that fusion of the 2nd and 3rd centra, only present in some bariliines, may be synapomorphic for those taxa and other Cyprinidae.

Posterior myodome. Whilst it is recognised that a ventrally open posterior myodome often occurs in what are regarded as plesiomorphic teleosts (Patterson, 1975) it does not follow that the feature is itself plesiomorphic. Amongst otophysans, the posterior myodome in characoids is developed to various degrees. In some taxa currently recognised as monophyletic groups (Alestinae) there are some species with an open and others with a closed myodome. Also, in those taxa usually regarded as plesiomorphic (e.g. *Hepsetus*) the myodome is closed, whereas in those considered derived (Serrasalmidae) it is open. Ontogenetic evidence for polarity is contradictory; in a cyprinid investigated the myodome closes during ontogeny (*Opsariichthys*; see Howes, 1980), whereas in salmonids it opens (Verraes, 1974). Functionally, an open myodome serves to extend the length of the posterior eye muscles which then originate either from the rim of the basioccipital or from the anterior vertebrae. From its mosaic distribution and varying morphology, it is more parsimonious to suppose that an open posterior myodome has developed independently in several lineages, and as such is an unreliable indicator of relationship.

Hyomandibular flange, frontal fossa and *temporal foramen.* For the most part the same argument may be applied to these features as to the posterior myodome, namely, mosaic distribution through independent derivation, and thus I agree with Fink & Fink (1981) in disregarding them. However, some mention must be made of the lateral temporal foramen. Wu, Chen, Chen & Chen (1981) considered that the lateral temporal fossa in the Cobitidae and Gyrinocheilidae, and the supratemporal fossa in Catostomidae are homologues of the post-temporal fossa in other cyprinoids. This certainly appears to be so, as in all cases the fossa is bounded by the epioccipital, pterotic and, usually, the parietal. The lateral temporal foramen described in *Opsaridium* (Howes, 1980) is not to be confused with the above as it occurs between the pterotic and sphenotic and is thus homologous with that aperture in some characoids (e.g. *Salminus*).

Metapterygoid process. Although a metapterygoid dorso-posterior process occurs in other otophysans, it differs markedly from the condition considered derived for some bariliine taxa (Howes, 1980). In *Raiamas* the process is directed anterodorsally at an angle of 45° and is the same length as the upper part of the hyomandibula. Furthermore, the process has a gutter along its posterior border into which the *levator arcus palatini* muscle inserts. In other bariliines the process is not so well developed, but in *Engraulicypris* and *Leptocypris* it is tall and lamellate, occupying a mid-dorsal position on the metapterygoid. In these taxa it also serves to support the LAP muscle. Whilst it is accepted that a metapterygoid process is a common otophysan feature, in none does it possess the morphology of the process in bariliines, nor does it provide the site of attachment of almost the entire LAP muscle.

Vertebral fusion. Fink & Fink's (1981) claim that all other members of the bariliine group are '. . . more specialised than *Opsariichthys* in having the second and third centra fused' must be treated with caution.

Fusion of centra 2 and 3 is a variable character throughout the Cyprinidae. There may be only partial (dorsal) fusion, as in *Zacco* and *Engraulicypris* (Howes, 1980) and *Pseudolaubuca* (Howes, 1978). Monophyletic groups contain taxa exhibiting both fused and unfused centra (e.g. aspinines and squaliobarbines) and in such cases it is not always the more derived members of the groups which display the fusion pattern. Thus, vertebral fusion must be regarded as having been derived independently in several lineages. Supporting Fink & Fink's argument for the derived nature of vertebral fusion simply leads to an unresolved reticulate pattern of relationships (Fig. 2).

Interrelationships of bariliines

Disregarding the posterior open myodome and those characters considered by Fink & Fink (1981) as plesiomorphic, the bariliine group can be defined on only a single synapomorphy, *ie* a connection between the posttemporal and subtemporal fossae. That this character has now been found in *Salmostoma* (placed in the *cheline group* by Howes, 1979) revises the concept of the bariliine group.

Accepting the fossae connection as synapomorphic, then two lineages can be recognised, (1) those species with elongate pectoral and pelvic axial scales, long and expanded processes of the 1st vertebrae, with development of a condylar joint with the basioccipital, and a modified ethmo-vomerine region (see caption to Fig. 3), and (2) those with the pectoral and pelvic axial scales lobate or fleshy, the rostral barbel attached to the lateral border of the palatine, parallel rows of tubercles on the lower jaw, and distinctive body and fin patterning.

Lineage (1) includes *Barilius barila, B. evezardi, B. modestus* and *B. vagra, Salmostoma, Engraulicypris, Raiamas* and *Leptocypris. Salmostoma* was regarded by Howes (1979) as the plesiomorph sister group of 'cheline' genera. The 'chelines' share with *Barilius* and *Salmostoma* the derived form of anterior vertebrae and ethmovomerine region, but lack the

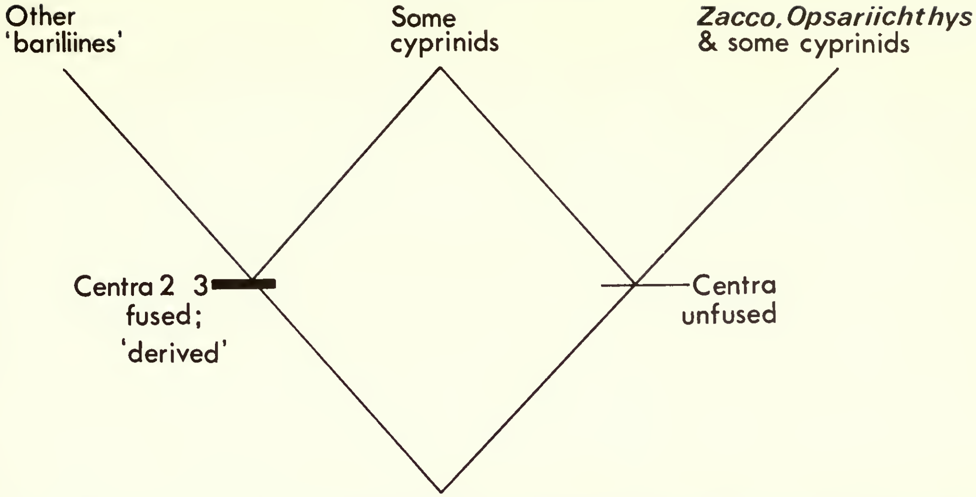
Other 'bariliines'
Some cyprinids
Zacco, Opsariichthys & some cyprinids
Centra 2 3 fused; 'derived'
Centra unfused

Fig. 2 A cladogram of cyprinid relationships based on the pattern of vertebral fusion proposed by Fink & Fink (1981); see text.

posttemporal-subtemporal connection. *Salmostoma,* however, shares with all other chelines a deep, posteriorly sloped neural complex. Only one 'cheline' genus, *Securicula* shares the elongate pectoral and pelvic axial scales with *Salmostoma* and *Barilius.* In the absence of synapomorphies linking the 'cheline' genera with any other cyprinid taxon, the absence of these features is considered as a phylogenetic loss. Current observations indicate that the genera *Rastrineobola, Neobola* and *Chelaethiops* also belong to this lineage, and work in progress attempts to define more precisely the relationships of these three genera.

Lineage (2) contains the remaining *Barilius* species—recognised as group (ii) by Howes (1980 : 180)—together with *Opsaridium, Opsariichthys* and *Zacco,* plus the luciosomine genera (*sensu* Howes, 1980).

In summary, it would seem that the bariliine and cheline groups (*sensu* Howes, 1979; 1980) are paraphyletic assemblages; a revised hypothesis of the interrelationships of the relevant taxa is presented in Fig. 3.

The dates of *Opsaridium* Peters and *Rastrineobola* Fowler

Jordan (1919) mistakenly gives the publication date of *Opsaridium* Peters as 1855. Howes (1980) followed this error. The correct date is 1853 (see citation in references). The specific name is correctly *zambezensis.*

The publication date of *Rastrineobola* Fowler is 1936, not 1934 as misprinted in Howes (1980 : 195).

Bengala Gray, 1832, a senior synonym of *Megarasbora* Günther, 1868

Günther (1868) established the genus *Megarasbora* to contain *Cyprinus elanga* Hamilton, 1822. *Megarasbora* was recognised by Brittan (1954) and Howes (1980) in their respective revisions and reviews of rasborine cyprinids. However, all three authors had overlooked the fact that Gray (1832) had already established the genus *Bengala* for Hamilton's species. Jordan (1919) recorded *Megarasbora* as a junior synonym of *Bengala.*

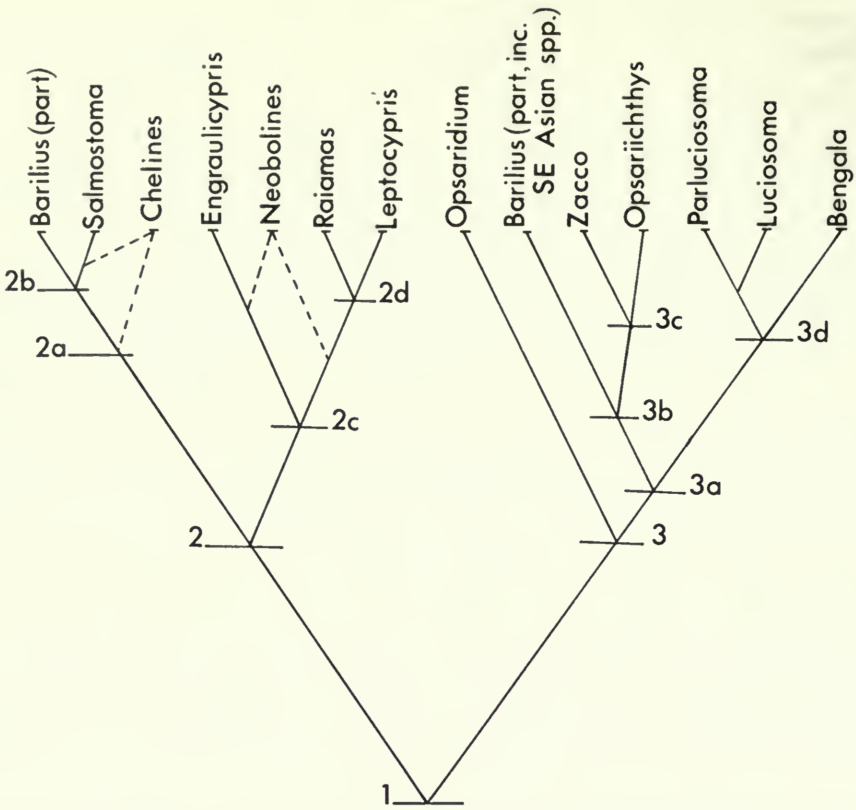
Barilius (part)
Salmostoma
Chelines
Engraulicypris
Neobolines
Raiamas
Leptocypris
Opsaridium
Barilius (part, inc. SE Asian spp.)
Zacco
Opsariichthys
Parluciosoma
Luciosoma
Bengala
2b
2a
2d
2c
2
3c
3b
3d
3a
3
1

Fig. 3 Revised cladogram of 'bariliine' and 'cheline' relationships (dashed lines indicate uncertain affinities). 1, posttemporal–subtemporal fossa connection; 2, pectoral and pelvic axial scales elongate (lost in 'chelines' and *Engraulicypris*); 2a, 1st vertebra with expanded lateral processes; 2b, omega-shaped ethmoid notch, vomerine arms extending straight forward; 2c, reduction of dilatator fossa, derived condition of jaw adductor muscles; 2d, loss of *intermandibularis* muscle, jaw elongation, hypertrophy of metapterygoid spine; 3, pectoral and pelvic axial scales lobate or fleshy; 3a, palatine extended laterally, supports rostral barbel (when present); 3b, parallel rows of tubercles on dentary; 3c, dentary with anterior notch, sexual dimorphism exhibited by extension and expansion of anal fin rays in males; 3d, bowl-shaped depression in supraethmoid. Characters described in Howes (1980), except 2b and 2c, taken from work in preparation.

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British Museum (Natural History)
An Atlas of Freshwater Testate Amoebae

C. G. Ogden & R. H. Hedley

1980, Hardcovers, 222pp, £17.50 (£18.00 by post). Co-published by British Museum (Natural History) and Oxford University Press.

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J. E. Hill

Zoology series Vol 45 No 3 25 August 1983

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J. E. Hill
Department of Zoology, British Museum (Natural History), Cromwell Road, London SW7 5BD

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Synopsis

Accessions of Indo-Australian bats to the collections of the British Museum (Natural History) during the past fifteen years are reviewed in detail, with a particular reference to the collections made in Papua New Guinea and Sulawesi by 'Operation Drake'. Numerous species and species groups from the region are examined and in some cases revised; a new species of *Hesperoptenus* from Sulawesi and a new subspecies of *Myotis adversus* from the New Hebrides are described. The more important taxonomic studies and notes made in this study and the new range records that it reports are listed in a terminal summary.

Introduction

A variety of collections of bats from the region bounded by India in the west and the New Hebrides, New Caledonia and Fiji to the east has been received at the British Museum (Natural History) during the years 1967–1982. Some have come from individuals who have obtained small numbers of bats while visiting the region, others from large, organised expeditions that have carried out biological studies, or by donation from workers connected with organisations and institutions in the area. Individually much of this newly accessed material scarcely justified separate publication and record, although often unusual or of taxonomic or faunal interest.

Towards the end of this period, however, extensive collections of bats were made in Papua New Guinea and in Sulawesi by Mr Ben Gaskell, an ecologist and collector with 'Operation

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Drake', the commemorative round-the-world voyage of the brigantine *Eye of the Wind* in 1978–1980 that marked the 400th anniversary of the circumnavigation of the world by Sir Francis Drake in the *Golden Hind*. The voyage was interrupted from time to time so that the scientists, technicians and young people aboard could undertake adventurous, scientific or voluntary aid projects in various parts of the world. Bats were collected in Indo-Australia during two of these periods, first at and around Buso and Wau in Morobe Province, Papua New Guinea, and later in central Sulawesi, chiefly around Morowali where the objective was ultimately to prepare a Management Plan for the Morowali Nature Reserve.

The study of the specimens obtained by 'Operation Drake', especially of those from Sulawesi, has entailed a further and more wide-ranging examination of much of the Indo-Australian bat collection already in London, and has prompted a further examination of the more recently accessed material that has not before been reported in the literature. In particular it has led to further study of a number of long standing taxonomic problems in the area and to some taxonomic changes. Although basically this paper is concerned with specimens obtained through the explorations initiated and carried out through 'Operation Drake' it has thus been possible to add a variety of other studies and notes drawn from material from other localities and sources, much of it directly relevant to the 'Drake' collections.

Place names in many parts of the Indo-Australian region can present difficulties, there being sometimes a choice of as many as three variants of any one designation. In general the traditional and conventional European spelling or usage (i.e. Amboina, Ceram) has been adopted but Sulawesi has been used throughout for Celebes, this name having come into general use: however, the New Hebrides remain so called, although recently renamed Vanuatu. The Indonesian part of New Guinea appears as West Irian, while Papua New Guinea is used for the rest of the island: here, 'Province' has been omitted from locational data so that localities appear as 'Wau, Morobe' i.e. Wau, Morobe Province. Further west, Borneo is used as a general term for the entire island, divided into Sarawak, Sabah, Brunei and Kalimantan.

Measurements of specimens are in millimetres and with the exception of those of individual teeth have been made with a dial-reading micrometer. Teeth have been measured with a mechanical stage fitted to a stereoscopic microscope. Although no standard suite of external and cranial measurements has been used, conventional measurements are given where required, amplified in particular cases to conform with those employed by the describer or by previous workers on the species concerned. To avoid repetition, a notation has been adopted for the wing elements whereby III^m for example indicates the metacarpal of the third digit, III^1 its first phalange, III^2 its second: when length measurements of these elements are given in the text these designations appear without preamble.

Systematic Section

MEGACHIROPTERA

PTEROPODIDAE

PTEROPODINAE

Rousettus amplexicaudatus stresemanni Stein, 1933

Rousettus stresemanni Stein, 1935: 91. Japen (=Jobi) I, Geelvinck Bay, NE West Irian.

SPECIMENS EXAMINED. Papua New Guinea: ♂ BM(NH) 69.1416 Madang, 5° 14′S, 145° 45′E (skin, skull; coll. J. I. Menzies); ♂ BM(NH) 73.1967 Rauit, West Sepik, 525 m, 3° 36′S, 142° 15′E (in alcohol;

coll. Aberdeen University Exploration Society Expedition to New Guinea, 1973); 3♂♂ BM(NH) 78.850–852 Baku Forest Station, Gogol Valley, Madang (78.850, 851 in alcohol, skull of 78.850 extracted, 78.852 skin only; coll. P. A. Morris); ♀ BM(NH) 78.853 Baiyer R, c. 50 km NW of Mt. Hagen, Western Highlands (in alcohol, skull extracted; coll. P. A. Morris).

Remarks. Until recently there have been few records of *stresemanni* and for many years (Laurie & Hill, 1954) it has been considered a distinct species co-existing in New Guinea with *R. amplexicaudatus brachyotis* (Dobson, 1877). Latterly, however, a number of reports from Papua New Guinea has appeared, McKean (1972) recording a series of *stresemanni* from Ihu, Greig-Smith (1975) a specimen (listed above) from Rauit, with a record of an example (also listed above) from Madang first noted (in litt.) by Menzies, and with Koopman (1979) reporting material from Bagabag I, off the northeastern coast near Madang and later (1982) from Dabora, Tapio and Mornuna, Milne Bay, east Papua New Guinea. Menzies (1977) tentatively referred sub-fossil remains from Kiowa in Ghimbu Province to *stresemanni*. Finally, Rookmaaker & Bergmans (1981) have listed numerous records from localities in much of New Guinea, some evidently based on specimens previously identified as *R. a. brachyotis*. Specimens in the American Museum of Natural History suggested to Koopman (1979) that *stresemanni* might be properly regarded as a subspecies of *R. amplexicaudatus* while Rookmaaker & Bergmans (1981) in their comprehensive review of this species have synonymised *stresemanni* with *R. a. amplexicaudatus* (Geoffroy, 1810*a*).

Specimens recorded here from Papua New Guinea are large, corresponding closely with the original description of *stresemanni* by Stein. In size they also agree with specimens from Ihu reported by McKean (1972) and with those from New Guinea measured by Rookmaaker & Bergmans (1981). They are generally a little larger than six from Timor examined by Goodwin (1979) and are similarly near or exceed the upper size limits of Timorese specimens (including some of those seen by Goodwin) studied by Rookmaaker & Bergmans. Specimens from Timor may be assumed to be topotypical or nearly so of *R. a. amplexicaudatus*, described originally from that island. The dimensions given by Rookmaaker & Bergmans for examples from New Guinea are likewise generally a little greater than those for specimens from Timor and its associated islands.

External measurements of 4♂♂ and 1 ♀, with cranial measurements of 2♂♂ and 1 ♀: length of forearm 85·8–90·4, 85·5; greatest length of skull 38·6, 39·4, 38·8; condylobasal length 36·8, 37·0, 37·5; condylocanine length 35·6, 35·8, 36·0; length front of orbit to tip of nasals 13·1, 13·0, 13·1; length palation to incisive foramina —, 17·5, —; least interorbital width 8·6, 8·3, 8·3; least postorbital width 7·5, 7·6, 8·3; zygomatic width 24·7, 24·0, 22·3; width of braincase 15·4, 15·6, 15·4; mastoid width 14·6, 14·1, 14·4; greatest width c^1–c^1 7·1, 7·4, 7·6, c^1–c^1 (alveoli) 6·7, 6·9, 7·0; m^2–m^2 (alveoli) 10·2, 10·3, 10·8; c–m^2 13·5, 13·7, 14·0; length complete mandible from condyles 28·6, 28·3, —; length right ramus from condyle 30·1, 29·9, 30·0; c–m_3 15·1, 14·7, 15·6.

Discussion. Rookmaaker & Bergmans (1981) have reviewed *R. amplexicaudatus* in detail, with a summary of earlier classification, synonymies, and many measurements derived from a relatively large number of specimens. These authors considered size to be the only major subspecific character in the species and recognised three size groups from the Solomon Islands, New Guinea, the Philippine Islands, Timor and Java. Of these, the smallest examples were found to occur on the Solomon Islands, the largest in New Guinea and the Philippines (these latter being mutually indistinguishable); specimens from Java, like those from the Solomons, proved significantly smaller than specimens from New Guinea and the Philippines. Examples from Timor were found to be generally a little larger than those from Java, but not significantly so, and a little smaller on the whole than those from New Guinea and the Philippines, although again the differences lacked significance. However, such specimens were thought by Rookmaaker & Bergmans to have a greater similarity to examples from New Guinea and the Philippines than to those from Java. On this basis they recognised three subspecies, *R. a. brachyotis* (Dobson, 1877*a*) from the Solomon and Bismarck Islands, *R. a. infumatus* (Gray, 1870) from Sumatra and Java east to Flores and possibly Alor Island,

and *R. a. amplexicaudatus* from Sumba Island, Timor and some smaller associated islands, New Guinea, possibly from the Molucca Islands, and from the Philippines. Specimens from Sulawesi were not allocated to subspecies: others from Borneo, Mentawei and Engano Islands, Malaya, Thailand and Burma were referred to *R. a. amplexicaudatus,* but few examples are available from the western part of the range. At the eastern limit, however, Smith & Hood (1981) have suggested that the population on the Bismarck Islands (*R. a. brachyotis*) is subspecifically separable from that on the Solomon Islands (*R. a. hedigeri* Pohle, 1953), although the distinction is less marked than the divisions between these island subspecies and *R. a. stresemanni* from New Guinea.

Considerations of relative size led Rookmaaker & Bergmans (1981) to associate specimens from Timor with those from New Guinea and thus to synonymise *stresemanni* with *R. a. amplexicaudatus.* However, their account of specimens from Sulawesi and some of its associated islands indicates that in some ways these unallocated examples are intermediate between *R. a. infumatus* and Timorese specimens of *R. a. amplexicaudatus.* A study of their detailed tabulated measurements for these populations confirms this view: also of two specimens (BM(NH) 98.11.3.20–21) from Alor Island provisionally allocated to *R. a. infumatus* by Rookmaaker & Bergmans the male is similar in size to males from Timor, but the female to females from Java. Rookmaaker & Bergmans also made a detailed examination of the relation between condylobasal length and zygomatic width in some of the populations of *R. amplexicaudatus.* Their diagrams show that while in these dimensions Timorese specimens lie in the lower part of the range of variation of those from New Guinea and the Philippines and are separated more distinctly from the Javanese population the limited Sulawesian sample tends to bridge this interval. It is also evident that the majority of specimens from New Guinea and the Philippines exceed Timorese and Sulawesian specimens in one or both of these dimensions. There seems, therefore, at least as much to justify the association of Timorese specimens (*R. a. amplexicaudatus*) with those from Sumatra, Java and the Lesser Sunda Islands (*R. a. infumatus*) as with those from New Guinea.

For these reasons *stresemanni* has been retained as a distinct subspecies in New Guinea and possibly also in the Philippine Islands. Measurements by Rookmaaker & Bergmans (1981) indicate that only small overall differences exist between these populations. Philippine females have longer wing elements than the very limited New Guinea sample examined and on the basis of a larger representation of females from New Guinea are cranially rather smaller on the whole but with longer toothrows. Until more specimens are available from the Molucca Islands, Sulawesi and the western part of the range of *R. amplexicaudatus* from Borneo and Sumatra to Burma it seems appropriate to regard *R. a. amplexicaudatus* as a valid link between the smaller *R. a. infumatus* and the larger *R. a. stresemanni.*

Rousettus celebensis Andersen, 1907

Rousettus celebensis Andersen, 1907*a*: 509. Mount Masarang, N Sulawesi, 3500 ft.

SPECIMENS EXAMINED. N Sulawesi: ♀♀BM(NH) 78.964–967 Tangkopo, Batuangus, near Bitung (in alcohol, BM(NH) 78.965 head, skin, others heads only; coll. A. M. Jones).

C Sulawesi: ♂♂ BM(NH) 81.1066–1068 Ganda Ganda, 1° 57′ S, 121° 21′ E; ♂ BM(NH) 81.1069 Sampalawa, 21 km from Kolono Dale, c. 2° 00′ S, 121° 20′ E: 5 ♂♂, 11 ♀♀ BM(NH) 81.1070–1085 R Ranu, 1° 51′ 121° 30′ E; 2♂♂ (yg.), 2♀♀ BM(NH) 81.1086–1089 Songinbau, 1° 46′ S, 121° 43′ E; 2 ♀♀ BM(NH) 81.1090–1091 Taronggo, 1° 44′ S, 121° 40′ E (all in alcohol; coll. B. H. Gaskell, 'Operation Drake').

REMARKS. Andersen (1907, 1912) pointed out that this species had before then been confused with *R. brachyotis* (=*R. amplexicaudatus brachyotis*) and indeed earlier authors also referred specimens since recognised as *celebensis* to *R. amplexicaudicaudatus* or to *R.*

minor Andersen, 1907 (=*R. amplexicaudatus infumatus,* after Rookmaaker & Bergmans, 1981). Andersen's view (1912) that the alleged occurrence of *R. amplexicaudatus* (as *R. brachyotis*) in Sulawesi probably rested on confusion with *R. celebensis* may well have led to all *Rousettus* from that island being referred to the latter species, as Rookmaaker & Bergmans (1981) suggest. These authors record specimens of *R. amplexicaudatus* from Gorantalo and Talassa in Sulawesi and from the associated islands of Muna, Peleng and Talisai: those from Peleng were referred originally to *R. amplexicaudatus* by Tate (1942*c*). The two species may be distinguished by a number of features: *celebensis* has longer fur, a furred notopatagium and much more densely pilose tibiae while the rostrum is relatively longer with longer, more nearly parallel rather than convergent upper toothrows. The dentition also provides good diagnostic features: the last upper premolar (pm^4) is longer than in *amplexicaudatus* and the molars both above and below are distinctly narrow, the crowns of $m\frac{1}{1}$ and m_2 clearly elongate, m_1 in particular being longer than in *amplexicaudatus.*

Rookmaaker & Bergmans (1981) reported and examined a total of 28 Sulawesian specimens (including BM(NH) 78.964–967) of *R. celebensis,* with 10 further examples from the Sanghir (=Sangihe) Islands and one from either the Talaud or Sanghir Islands: they do not include the holotype or two others listed by Andersen (1912). Among this material there is one extensive series, of 18 examples collected by G. Stein at Makassar. Specimens from 'Operation Drake' and others reported here therefore considerably extend the known representation of the species. They agree closely with the accounts by Andersen (1907, 1912): one, BM(NH) 81.1068 is unusual in lacking the right upper molar (M^2) and in having only four instead of six cheekteeth in the left lower jaw, there being no trace of the last two molars (m_2, m_3), while BM(NH) 81.1075 and BM(NH) 81.1091 are young adults with the last molars ($m\frac{2}{3}$ yet to erupt. Length of forearm in 8 adult ♂♂ 71·8–76·9 (74·9); in 14 adult ♀♀72·5–80·2 (76·5). Males fall within the range of forearm lengths given by Rookmaaker & Bergmans (1981) for a slightly larger sample of male examples, but some females exceed the upper limit of the female specimens measured by these authors. Andersen (1912), who may have examined only dry skins, thought that the species might have a long tail, its length probably about 20 mm. The length of the tail in 8 ♂♂ is 23·5–27·5 (25·3) and in 14 ♀♀ 23·1–30·0 (27·1).

DISCUSSION. I am unable to agree with Tate (1942*c*), who had seen only Andersen's description, that *celebensis* appears to be a member of the *amplexicaudatus* group, with narrower molars, and who in fact suggested that *celebensis* might be a subspecies of *R. amplexicaudatus* although listing it formally as a valid species. Koopman (1979) in discussing the status of *stresemanni* which he considers a subspecies of *R. amplexicaudatus* has pointed out that *celebensis* is distinct, an opinion fully endorsed by Rookmaaker & Bergmans (1981) who record both *amplexicaudatus* and *celebensis* from Gorontalo in N Sulawesi.

Andersen (1912) recognised three subgenera in *Rousettus,* placing both *amplexicaudatus* and *celebensis* in the nominate subgenus, distinguished by moderate deflection of the braincase, the last upper premolar (pm^4) not especially narrowed, its width about one third of the palatal width between the fronts of pm^{4-4}, the wing originating from the back of the first toe, and by a distinct antitragal lobe. In contrast, the subgenus *Stenonycteris* was defined by Andersen chiefly on the basis of a strongly deflected braincase, excessively narrow cheekteeth with the width of pm^4 about one fifth of the palatal width between the fronts of pm^{4-4}, wings originating from the back of the second toe and obsolete antitragal lobe.

In many respects *R. celebensis* approaches the African *R. lanosus* Thomas, 1906*a* apparently the sole representative of Andersen's subgenus *Stenonycteris.* It has similarly long, rather dense pelage extending on to the notopatagium, with long hairs on the forearms, tibiae, interfemoral membrane and the underside of the lateral membrane; long thumbs and long wings that tend towards those of the African species (wing indices of *celebensis* appear in Table 1); the wing is inserted at or near the rear of the second toe; a small, reduced, rounded antitragal lobe; the basicranial axis is somewhat deflected; the cheekteeth are gener-

Table 1 Wing indices (length of forearm = 1000) of 7 ♂♂ and 14 ♀♀ of *Rousettus celebensis*.

		Range	Mean
Thumb	♂♂	393–439	423
	♀♀	388–458	409
II^{m}	♂♂	444–480	458
	♀♀	427–471	446
II^{1}	♂♂	106–125	117
	♀♀	93–128	108
II$^{2-3}$	♂♂	116–142	133
(c.u.)	♀♀	110–142	128
III^{m}	♂♂	651–669	658
	♀♀	636–694	660
III^{1}	♂♂	455–469	462
	♀♀	438–474	455
III^{2}	♂♂	548–621	585
	♀♀	554–615	583
IV^{m}	♂♂	631–652	637
	♀♀	617–659	635
IV^{1}	♂♂	330–356	344
	♀♀	321–359	340
IV^{2}	♂♂	368–401	378
	♀♀	343–385	367
V^{m}	♂♂	623–651	639
	♀♀	615–645	637
V^{1}	♂♂	291–306	299
	♀♀	275–304	292
V^{2}	♂♂	333–355	348
	♀♀	325–352	321

ally long and narrow, and, as in *lanosus*, the molars have little cuspidation. Andersen (1912) considered that *celebensis* probably represented a modification of the *R. amplexicaudatus* type, but it seems more appropriate to include this Sulawesian species with *R. lanosus* in the subgenus *Stenonycteris* if this is to be recognised rather than in the nominate subgenus where Andersen originally placed it.

Pteropus hypomelanus macassaricus Heude, 1896

Pteropus macassaricus Heude, 1896 : 177, footnote, pl. 5, fig. 4. Makassar, S Sulawesi.

SPECIMENS EXAMINED. C. Sulawesi: ♂ BM(NH) 81.1092 Ganda Ganda, 1° 57′ S, 121° 21′ E; ♀♀ BM(NH) 81.1093–1096 1 km NE of Tandiondo, 1° 45′ S, 121° 17′ E (all in alcohol, all except BM(NH) 81.1092 heads only; coll. B. H. Gaskell, 'Operation Drake').

Pteropus alecto alecto Temminck, 1837

Pteropus alecto Temminck, 1837, 2 : 75. Menado, N Sulawesi.

SPECIMENS EXAMINED. C Sulawesi: ♂, 4 ♀♀ BM(NH) 81.1097–1101 1 km NE of Tandiondo, 1° 45′ S, 121° 17′ E (in alcohol, heads only; coll. B. H. Gaskell, 'Operation Drake').

Remarks. Musser *et al.*(1982) have demonstrated that among the several forms of *Pteropus* described or reported from Sulawesi *P. arquatus* Miller & Hollister, 1921 is in fact *Acerodon celebensis,* as are the specimens from the northern part of the island recorded originally by Tate (1942*c*) as *P. argentatus.* Others known from Sulawesi besides *P. hypomelanus macassaricus* and *P. alecto alecto* are *P. griseus mimus* Andersen, 1908, *P. caniceps dobsoni* Andersen, 1908 and *P. personatus* Temminck, 1825.

Pteropus conspicillatus Gould, 1850

Pteropus conspicillatus Gould, 1850 : 109. Fitzroy I, Queensland, Australia.

Specimens examined. Papua New Guinea: ♂, ♀, ♀ juv. BM(NH) 80.525–527 Lababia Cave, Lababia I, Morobe, 7° 15′ S, 147° 09′ E (in alcohol, coll; B. H. Gaskell, 'Operation Drake').

Remarks. Laurie & Hill (1954) listed *P. c. conspicillatus* from Papua New Guinea after Matschie (1899) who reported this subspecies from Bongu (5° 30′ S, 145° 50′ E) and Madang (5° 13′ S, 145° 48′E): a second subspecies, *P. c. chrysauchen* Peters, 1862 was listed from northwestern New Guinea after Tate (1942*c*) who recorded it from Geelvinck Bay.

These examples from Lababia Cave cannot be allocated positively to either of these subspecies. The adult ♂ BM(NH) 80.525 has a uniformly dark head, the forehead, crown and sides of the muzzle blackish, mixed especially on the forehead and on the muzzle anterior to the eyes with buffy hairs. Beyond a slight band of buffy hairs there is no indication of the paler eye rings characteristic of *P. c. conspicillatus* and the sides of the muzzle are not pale as in this subspecies. The adult ♀ BM(NH) 80.526, however, although predominantly black on the forehead, crown and cheeks has relatively distinct paler buffy eye rings and the sides of the muzzle above the mouth and the corresponding areas along the lower jaw are distinctly ochraceous buff. Moreover, the black of the crown extends forward as an acutely triangular patch whose apex intrudes between the pale superciliaries to the base of the rostrum. The adult male agrees therefore with *P. c. chrysauchen,* the adult female with *P. c. conspicillatus.* The collections of the British Museum (Natural History) include two further specimens (♂, ♀ 22.1.22.1–2) from Simbang, on the east coast of Papua New Guinea (probably at 3° 35′ S, 147° 43′ E) that are referable to *P. c. conspicillatus* although even in these the facial markings of the male are a little less pronounced than in the female example. Length of forearm in specimens from Lababia Cave (♂, ♀) 181, 179.

Styloctenium wallacei (Gray, 1866)

Pteropus wallacei Gray, 1866*a* : 65, fig. 1. Makassar, S Sulawesi.

Specimens examined. C Sulawesi: ♀ (yg. ad.), ♂ BM(NH) 81.1102–1103 R Ranu, 1° 51′ S, 121° 30′ E (in alcohol); ♂ (yg. ad.) BM(NH) 81.1104 (in alcohol), ♀ BM(NH) 81.1105 (skin, skull, skeleton), ♀ (yg.) BM(NH) 81.1106 (in alcohol) Tambusisi Damar, Mt. Tambusisi, c. 4000 ft, 1° 39′ S, 121° 22′ E (all coll. B. H. Gaskell, 'Operation Drake').

Remarks. Although this distinctive bat is by no means common in collections there is a number of records (Jentink, 1883; Matschie, 1899; Andersen, 1912) from N Sulawesi and Tate (1942*c*) has reported a long series from Malenge in the Togian Islands in the Gulf of Gorantalo. There is also a hitherto unreported specimen (♂ MZB 12671) from Titaeli, Minahassa, in the collections of the Museum Zoologicum Bogoriense, Bogor.

Adults obtained by Operation Drake display very clearly the badger-like white facial markings characteristic of the species: the white shoulder patches although always present are rather small in the two male examples, one not quite fully adult.

External measurements of an adult ♂ and ♀ (BM(NH) 81.1103, 81.1105): length of forearm 96·6, 95·5; thumb (c. u.) 43·2, 42·3; I^m 12·2, 12·0; I^1 23·7, 23·4; II^m 50·7, 51·5; II^1 12·4, 12·3; II^{2-3} (c. u.) 12·0, 11·3; III^m 69·0, 67·2; III^1 51·3, 51·4; III^2 69·0, 63·7; IV^m 69·4, 68·6; IV^1 39·7, 38·5; IV^2 40·6, 40·4; V^m 71·7, 71·8; V^1 31·4, 31·5; V^2 33·8, 33·9; tibia 42·4,—. Cranial measurements of an adult ♀ (BM(NH) 81.1105): total length of skull to gnathion 51·8; condylobasal length 48·5; condylocanine length 44·4; length front of orbit–tip of nasals 16·8; palatal length 28·0; length palation–incisive foramina 23·8; length palation–basion 18·3; lachrymal width 10·5; least interorbital width 6·8; least postorbital width 5·9; zygomatic width 28·3; width of braincase 19·7; mastoid width 17·9; orbital diameter 11·4; c^1–c^1 (crowns) 9·5, (alveoli) 8·8; m^1–m^1 (crowns) 13·9, (alveoli) 12·7; c^1–c^1 (internally, cingula) 5·1; pm^4–pm^4 (internally) 6·9; width of mesopterygoid fossa 7·4; c–m^2 19·1; length of complete mandible from condyles 36·4; length right ramus from condyle 38·1; coronoid height 19·8; c–m_2 19·9.

Dobsonia viridis (?) viridis (Heude, 1896)

Cephalotes viridis Heude, 1896 : 176, footnote, pl. 5, fig. 1. Kei Is.
Dobsonia viridis umbrosa Thomas, 1910*a* : 384. Ceram I.

SPECIMENS EXAMINED. C Sulawesi: ♀, ♂ BM(NH) 81.1107–1108 R Ranu, 1° 51′ S, 121° 30′ E (in alcohol, skulls extracted; coll. B. H. Gaskell, 'Operation Drake').

REMARKS. These are apparently the first of *viridis* to be reported from Sulawesi: it occurs otherwise on the Kei Islands and on the islands of Amboina, Buru, Ceram and Banda. Thomas (1910*a*) separated specimens from Ceram as *D. v. umbrosa* to which Andersen (1912) subsequently referred others from Buru and Amboina: this author (p. 825) remarked that the reference by Thomas to a number of specimens from 'Aru' is a misprint for Buru but in his personal copy of his paper, now in the Library of the British Museum (Natural History), Thomas has corrected Aru to Kei [Islands]. The collections in London include several specimens collected by W. Stalker on the Kei Islands but only a single immature from Buru, obtained by this collector. A small average difference in colour separates *umbrosa* from *viridis* of the Kei Islands and the two are synonymised in the listing by Laurie & Hill (1954). A closely related form, *D. crenulata* Andersen, 1909 occurs on the Halmahera group of islands to the northwest of New Guinea and has been reported recently from the Sanghir (=Sangihe) Islands and on the Togian Islands. It is separated from *D. viridis* chiefly on account of its greater size and larger teeth.

Specimens from Sulawesi have the characteristic dentition of the *viridis* group of Andersen (1909, 1912) in which m^1 has a well-developed antero-internal ledge and pm^4_4 and m^1_1 have cuspidate labial and lingual ridges. The surface cusps or ridges of m^1_1 and m_2 are also strongly developed and prominent, of pm^4 much less so. The collector, B. H. Gaskell remarks of the coloration of the adult that when freshly obtained the dorsal pelage was a light dull green in hue, yellower towards the rear and flanks, with the upper surface of the head yellowy green grey, sharply divided on the neck from the colour of the body. The ventral surface was generally similar in colour to the lower back but medially light orange. The indefinite greenish tinge in the pelage appears characteristic of *D. viridis*: Goodwin (1979) also commented upon the unusual olive green colour of adults of *D. peronii peronii* (Geoffroy, 1810*a*) when living. The colour faded rapidly in specimens preserved as dry skins, in alcohol, or in formalin.

In size both Sulawesian examples are similar to or exceed the largest of Moluccan specimens of *viridis* and their cheekteeth, especially of the male, are generally longer and slightly larger, particularly pm^4, $m\frac{1}{1}$ and m_2. To some extent, therefore, they approach *crenulata* but their canines are smaller and their cheekteeth generally narrower, like those of *viridis* from the Moluccas.

Measurements of an adult ♀ and ♂ (BM(NH) 81.1107–1108): length of forearm 113·5, 125·4; III^m 71·6, 77·1; IV^m 65·4, 70·0; V^m 66·2, 71·0; total length of skull to gnathion 48·2, 50·1; condylobasal length 46·2, 47·8; condylocanine length 45·7, 47·6; rostral length 15·6, 15·3; length front of orbit–tip of nasals 12·2, 11·9; palatal length 24·1, 25·0; length palation–incisive foramina 21·1, 22·1; length palation–basion 19·1, 19·6; lachrymal width 11·8, 11·6; least interorbital width 8·4, 8·2; least postorbital width 7·5, 6·4; zygomatic width 29·4, 31·1; width of braincase 19·7, 19·7; mastoid width 18·4, 18·3; orbital diameter 9·9, 9·9; c^1–c^1 (crowns) 9·3, 9·5, (alveoli) 8·7, 8·7; m^1–m^1 (crowns) 14·6, 15·1, (alveoli) 13·8, 14·4; m^2–m^2 (crowns) 12·8, 12·9, (alveoli) 12·5, 12·6; c^1–c^1 (internally, cingula) 3·4, 3·7; pm^4–pm^4 (internally, 7·6. 7·7; width of mesopterygoid fossa 6·0, 5·8; c–m^2 (crowns) 18·8, 19·8, (cingula) 18·4, 19·4; length complete mandible from condyles 36·5, 37·4; length right ramus from condyle 37·7, 38·9; coronoid height 20·3, 21·8; c–m_3 (crowns) 20·0, 20·7, (cingula) 19·8, 20·4. Length/width of: c^1 3·86/2·48, 3·82/2·54; pm^3 3·94/2·88, 4·02/3·22; pm^4 4·02/2·72, 4·32/3·14; m^1 5·15/2·44, 5·17/2·83; m^2 2·34/1·56, 2·37/1·61; c_1 2·64/2·17, 2·65/2·22; pm_2 1·40/1·34, 1·30/1·45; pm_3 3·72/2·31, 3·90/2·52; pm_4 4·02/2·53, 4·22/2·62; m^1 3·99/2·15, 4·21/2·35; m_2 3·30/2·08, 3·31/2·16; m_3 1·90/1·31, 1·85/1·43.

DISCUSSION. The *viridis* group of *Dobsonia* as proposed by Andersen (1909, 1912) includes besides *D. viridis* and *D. crenulata* the further species *D. praedatrix* Andersen, 1909 from the Bismarck Archipelago and *D. inermis* Andersen, 1909 and *D. nesea* Andersen, 1909 from the Solomon Islands. Since Andersen wrote a number of changes have been made to this classification. Troughton (1936) regarded *nesea* as a subspecies of *D. inermis* while Rabor (1952) in describing *D. viridis chapmani* from Negros Island in the Philippine Islands treated *crenulata* as a further subspecies of *viridis*. Pohle (1953) considered *crenulata* and *praedatrix* to be subspecies of *D. viridis* and *inermis* (including *nesea*) probably so. Laurie & Hill (1954) retained the arrangement of Andersen but united *nesea* with *inermis* as a subspecies.

More recently, Bergmans (1975) discussed the *viridis* group in some detail, describing a further species, *D. beauforti* from Waigeo Island in the northern Moluccas, and rejecting the views of Rabor and Pohle. Since then he has (1978) examined the group yet further and has established that *chapmani* does not fulfil the appropriate diagnostic criteria but seems more likely to belong to the *moluccensis* group. Moreover, Bergmans is now of the opinion that *praedatrix* and *inermis* (including *nesea*) differ sufficiently from the two (sic) other species that they should form one or two species groups by themselves. *Dobsonia beauforti* is said to be morphologically allied to *D. viridis* but is appreciably smaller in forearm and skull measurements, in size much like *D. inermis* from the Solomon Islands. No specimens of *D. beauforti* have been examined.

Only the holotype (BM(NH) 60.8.26.2) of *crenulata* is available for study in London. However, De Jong & Bergmans (1981) have reviewed this taxon, recording it for the first time from the Sanghir (=Sangihe) Islands and from the Togian Islands, and have provided measurements of a number of specimens. These authors refer to earlier views (Rabor, 1952; Pohle, 1953) that *crenulata* is a large subspecies of *D. viridis*, but regard the union of the two into the same species as premature, since specimens of each sex from any one population are as yet insufficient to establish its range of size variation. The specimens from Sulawesi approach and in some respects equal *crenulata* in external and cranial dimensions, but on the whole have slightly narrower cheek teeth similar in width to those of *viridis*. They have smaller canines than the subadult holotype of *crenulata*, corresponding closely to those of *viridis*. This limited sample therefore suggests strongly that *viridis* and *crenulata* are likely to prove conspecific, a view provisionally adopted here.

Dobsonia praedatrix Andersen, 1909

Dobsonia praedatrix Andersen, 1909 : 532. Duke of York I, Bismarck Archipelago.

SPECIMENS EXAMINED. Bismarck Archipelago: ♀, ♂, ♀ BM(NH) 69.304–306 Kareeba Plantation, Keravat, New Britain, 4° 18′ S, 152° 01′ E (skins, skulls; coll. J. I. Menzies).

REMARKS. These relatively recently collected specimens confirm the diagnostic features used by Andersen (1909, 1912) in separating *praedatrix* from *viridis* and *crenulata*. As pointed out by Andersen, the rostrum is heavily built and is broader and more massive, with a considerably wider interorbital region. The teeth of the male example are similar in size to those of the holotype but in the female specimens are generally slightly smaller, overall much as the teeth of *viridis*. Andersen (1912) observed correctly that pm$\frac{4}{4}$ in the holotype of *praedatrix*, however, are practically as large as in *crenulata* but in each of the specimens reported here these teeth are smaller than those of *crenulata* and are nearer in size to pm$\frac{4}{4}$ of *viridis*. The labial and lingual longitudinal ridges of pm$\frac{4}{4}$ and m$\frac{1}{1}$ are faintly cuspidate in BM(NH) 69.305 but scarcely if at all cuspidate in BM(NH) 69.304 and 69.306. The longitudinal ridges of these teeth in the holotype are slightly more cuspidate, but the teeth are little worn. As in *viridis*, *crenulata* and in the holotype of *praedatrix* m$\frac{1}{1}$ and m$_2$ have well developed surfacial cusps or ridges: the surface cusp of pm^4 is low and very undeveloped.

The three specimens closely resemble the holotype in colour. Dorsally, the shoulders and neck are brownish, strongly tinged with black in the male, the head blackish brown, this darker colour extending medially down the nape and neck in a narrow line; the ventral surface of the body is brownish drab, medially with a faint wash of brighter tawny olive, the underside of the neck and chin with a much sparser covering of longer, brownish hairs.

The male example is larger cranially than the two female specimens, adding support to Bergmans (1975) who suggested that sexual dimorphism in size might well occur in some at least of *Dobsonia*. Measurements of ♂ BM(NH) 69.305, ♀♀69.304, 69.306 in that order: length of forearm 116·3, 117·3, 112·2; total length of skull to gnathion 50·6, 48·3, 48·5; condylobasal length 47·6, 45·6, 45·5; condylocanine length 47·3, 45·2, 45·0; length front of orbit–tip of nasals 14·5, 13·3, 13·1; palatal length 25·5, 23·7, 24·2; length palation–incisive foramina 22·6, 21·7, 21·7; length palation–basion 19·1, 18·8, 18·5; lachrymal width 13·8, 12·8, 12·9; least interorbital width 10·1, 9·7, 10·0; least postorbital width 8·2, 7·7, 7·9; zygomatic width 31·4, 30·0, 30·4; width of braincase 20·4, 19·4, 19·6; mastoid width 19·0, 17·8, 17·8; orbital diameter 10·8, 10·8, 10·6; c^1–c^1 (crowns) 9·7, 9·4, 9·4, (alveoli) 9·2, 8·8, 8·8; m^1–m^1 (crowns) 15·5, 14·7, 14·1, (alveoli) 14·7, 14·0, 13·5; c^1–c^1 (internally, cingula) 4·0, 4·1, 3·9; pm^4–pm^4 (internally) 8·0, 7·8, 7·5; width of mesopterygoid fossa 5·8, 5·9, 5·5; c–m^2 20·0, 18·4, 18·5; length complete mandible from condyles 37·8, 36·0, 36·0; length right ramus from condyle 39·2, 37·2, 37·5; coronoid height 21·6, 21·7, 21·6; c–m$_3$ 21·1, 19·2, 19·3. Length/width of cheekteeth: pm^3 4·41/3·08, 4·04/2·81, 4·06/2·84; pm^4 4·22/3·14, 3·97/2·82, 3·95/2·83; m^1 5·31/2·74, 4·73/2·61, 4·70/2·72; m^2 2·45/1·64, 2·06/1·49, 2·15/1·42; pm$_2$ 1·39/1·55, 1·13/1·43, 1·24/1·44; pm$_3$ 4·09/2·61, 3·87/2·39, 3·84/2·32; pm$_4$ 4·42/2·78, 3·89/2·48, 4·01/2·46; m$_1$ 4·14/2·46, 3·60/2·21, 3·91/2·20; m$_2$ 3·31/2·37, 2·98/2·02, 2·96/2·01; m$_3$ 1·95/1·55, 1·79/1·46, 1·60/1·33.

DISCUSSION. Examination of these adult examples confirms that Bergmans (1975) correctly rejected the suggestion by Pohle (1953) that *praedatrix* should be allied subspecifically to *D. viridis*, but I am less convinced that it should be removed from the *viridis* group as the former author (1978) has since suggested. If dental characters are to remain the chief criteria by which the species of *Dobsonia* are classified, then *praedatrix* must be included in the *viridis* group as Andersen (1909, 1912) envisaged it, except that the degree of cuspidation of the longitudinal ridges of pm$\frac{4}{4}$ and m$\frac{1}{1}$ is less than is general in the group or is sometimes virtually absent. In this respect *praedatrix* approaches the *peronii* group of Andersen (loc. cit.) in which these ridges are simple, but m^1 reputedly lacks the well marked antero-internal basal ledge characteristic of the *viridis* group. The limited material of *D. peronii* in London indicates that in this species m^1 has at least a small antero-internal ledge and that the character may not be as emphatic as Andersen implied, although the ledge is much more developed in *D. viridis* and its allies. As Bergmans (1978) suggested, *D. peronii*, by current classification the sole member of the *peronii* group, may be more closely related to the *viridis* group than to any other but as this author pointed out, *D. peronii* differs from *D. viridis* and from its allies in the outline of the rostrum, which is lower, relatively longer and curves downward less abruptly from the braincase. Bergmans also remarked that within the *viridis* group *peronii* comes closest to the *viridis-crenulata-beauforti* (sub)group (sic) but dentally it seems to approach more closely to *praedatrix*. The greenish coloration of *D. viridis* when alive also appears in *D. peronii peronii* according to Goodwin (1979).

Bergmans (1978) advanced the opinion that the inclusion of *praedatrix* from the Bismarck Archipelago and *inermis* (including *nesea*) from the Solomon Islands in the *viridis* group indicated a disregard of zoogeographical considerations. I find no conviction in this assertion since the group as presently constituted occupies the arc of islands to the west, northwest, north and northeast of New Guinea, perhaps without interruption since some remain zoologically poorly known. A biogeographic model of this nature was suggested by Smith & Hood (1981). Indeed, if *D. peronii* is regarded as a member of the *viridis* group it then includes a succession of island species and subspecies extending from Nusa Penida (near Bali) in the west to the Solomon Islands in the east, but apparently excluding New Guinea.

These considerations suggest that the *peronii* and *viridis* groups of Andersen (1909, 1912) might be merged to form a *peronii* group that includes *D. peronii, D. viridis* and its close allies, *D. praedatrix* and *D. inermis*. It can be summarized:

D. peronii grandis Bergmans, 1978	Nusa Penida I, Sumbawa I.
D. peronii sumbana Andersen, 1909	Sumba I.
D. peronii subsp. (see Bergmans, 1978)	W. Flores I, Alor I, Wetar I, Babar I.
D. peronii peronii (Geoffroy, 1810*a*)	Timor I.
D. viridis (?) *viridis* (Heude, 1896)	Sulawesi, Amboina I, Buru I, Ceram I, Banda Is, Kei Is.
D. viridis (?) *crenulata* Andersen, 1909	Rau I, Morotai I, Halmahera I, Ternate I, Batchian I, Togian Is, Sanghir (=Sangihe) Is.
D. beauforti Bergmans, 1975	Waigeo I.
D. praedatrix Andersen, 1909	New Britain, New Ireland, Duke of York I.
D. inermis nesea Andersen, 1909	N and WC Solomon Is: Shortland, Alu, Ghizo, Rubiana, Bougainville, New Georgia.
D. inermis inermis Andersen, 1909	S and EC Solomon Is: San Christoval, Ugi, Ysabel, Rennell.

Phillips (1968) considered *nesea* a synonym of *inermis*, but McKean (1972) retained it as a valid subspecies on the basis of Troughton's (1936) assertion that *inermis* is darker in colour.

The occurrence of *D. viridis* in Sulawesi and (as *crenulata*) on the Togian and Sanghir Islands also has some bearing on Bergman's (1978) view of possible former distribution routes for *Dobsonia* towards the Lesser Sunda Islands. He suggested that *D. peronii* and *D. moluccensis* or their ancestors in these islands (there is only one local record of the latter, from Semau (=Samoa) Island, near Timor) might have originated from New Guinea (*moluccensis*) or from the Aru, Kei or Timorlaut Islands (*peronii*), possibly moving along former land bridges, or alternatively along a more northerly route through the southern Moluccas and Sulawesi. A species of the *moluccensis* group, *D. exoleta,* has been known from Sulawesi for many years and Bergmans pointed out that the concept of the more northerly route implied that it is the closest living relative of *D. peronii,* although he considered *exoleta* to be less closely related to *peronii* than to the members of the *viridis* group. If Bergman's views are accepted the presence of *D. viridis* in Sulawesi resolves this apparent paradox.

Dobsonia moluccensis moluccensis (Quoy & Gaimard, 1830)

Hypoderma moluccensis Quoy & Gaimard. 1830.1 : 86, Atlas, pl. 11. Amboina.

Specimens examined. Molucca Is: BM(NH) 75.2140 Lihura limestone caves, near Ruhuwa, SC Ceram I (crania, mandible, fragments, teeth; coll. R. F. Ellen).

Remarks. This cave material compares favourably with *D. m. moluccensis* from Buru, Amboina and Ceram. Length of c–m^2 (alveoli) in two examples 23·1, 23·5.

Dobsonia moluccensis magna Thomas, 1905

Dobsonia magna Thomas, 1905*a* : 423. Tamata, Mambare R, Papua New Guinea, 100 ft.

Specimens examined. Papua New Guinea: ♀ BM(NH) 69.307 Brown R, near Port Moresby, c. 9° 27′ S, 147° 08′ E; ♂ BM(NH) 69.308 Tupuselaia (=Tupuselei), 9° 33′ S, 147° 19′ E (both skins, skulls; coll. J. I. Menzies): ♂ BM(NH) 73.1969 Kairiru Ridge, centre of Kairiru I, near Wewak, East Sepik, c. 2000 ft; ♂ BM(NH) 73.1970 Victoria Bay, NW end of Kairiru I (both in alcohol; coll. Aberdeen University Exploration Society Expedition to New Guinea, 1973); BM(NH) 78.202–209 ? Near Mt. Hagen, Western Highlands (crania, damaged); BM(NH) 78.210–211 Baiyer R, Western Highlands (mandibles, damaged); BM(NH) 78.212–249 Tuman, Kubor Range, Western Highlands (crania, damaged); BM(NH) 78.250–255 Upper Lai Valley, Southern Highlands (crania, mandibles, damaged); ♀ BM(NH) 78.854 About 10 km S of Madang (in alcohol); ♂ BM(NH) 78.855 About 10 km S of Madang, c. 40 m (skin); ♂ BM(NH) 78.856 Baiyer R, c. 50 km NW of Mt. Hagen, Western Highlands, 1300 m (in alcohol) (all coll. P. A. Morris); BM(NH) 79.2015 (skin), BM(NH) 78.3004 (skull) Haelaelinga Settlement, on Was (=Wage) R, Nipa, Southern Highlands (coll. P. Sillitoe); ♂, ♀ BM(NH) 80.528–529 Buso, Morobe, 7° 17′ S, 147° 08′ E (in alcohol; coll. B. H. Gaskell, 'Operation Drake').

Remarks. The cranial and mandibular material BM(NH) 79.202–255 was obtained from kitchen middens: most show signs of heating or burning. The rear of the cranium in such specimens has been broken open to allow the extraction of the brain, a circumstance noted by Menzies (1977) of material from similar accumulations at the Kiowa and Yaku rock shelters.

Dobsonia exoleta Andersen, 1909

Dobsonia exoleta Andersen, 1909 : 531, 533. Tomohon, Minahassa, Sulawesi.

Specimens examined. C Sulawesi: ♂ BM(NH) 81.1109 Ganda Ganda, 1° 57′ S, 121° 21′ E (in alcohol, skull extracted); ♂ BM(NH) 81.1238 Tapu Waru, 1° 51′ S, 121° 22′ E (in alcohol) (both coll. B. H. Gaskell, 'Operation Drake').

Remarks. The relatively unworn dentition of BM(NH) 81.1109 agrees closely with the holotype (BM(NH) 99.10.1.4) and with the account by Andersen (1912). The antero-internal corner of pm^4 is developed into a conspicuous ledge with elevated rim; centrally the ledge is raised into a small cusp; pm^3 has a similar, narrower ledge; the antero-internal corner of m^1 is low and platform-like but little differentiated except by a shallow antero-internal notch in the longitudinal ridge; a slight antero-internal basal ledge in pm$_3$, rather more developed in pm$_4$; m$_1$ with simple lingual ridge, no trace of an antero-internal ledge or cusp. There is a well developed posterior basal ledge on pm^3, a similar but slightly narrower ledge on pm^4; pm$_3$ has likewise a slightly wider posterior basal ledge than pm$_4$. Median surface cusps or ridges are well developed in m$^1_1$ and m$_2$, in the latter the ridge extending uninterruptedly through the length of the tooth; there is a low surface cusp on the posterior face of pm^4 that is absent from the more eroded dentition of BM(NH) 81.1238.

Measurements (♂ BM(NH) 81.1109, ♂ 81.1238, skull of 81.1109): length of forearm 116·8, 116·7; total length of skull to gnathion 51·7; condylobasal length 49·9; condylocanine length 49·8; length front of orbit–tip of nasals 14·4; palatal length 25·8; length palation–incisive foramina 23·4; length palation–basion 20·8; lachrymal width 12·4; least interorbital width 8·4; least postorbital width 7·0; zygomatic width 31·8; width of braincase 20·3; mastoid width 19·5; orbital diameter 11·1; c^1–c^1 (crowns) 10·5, (alveoli) 9·7; m^1–m^1 (crowns) 16·9, (alveoli) 15·9; c^1–c^1 (internally, cingula) 4·1; pm^4–pm^4 (internally) 8·2; width of mesopterygoid fossa 6·1; c–m^2 22·0; length complete mandible from condyles 39·7; length right ramus from condyle 41·0; coronoid height 21·2; c–m$_3$ 23·3.

Discussion. Dentally *D. exoleta* agrees with *D. moluccensis* from the Molucca Islands, New Guinea and from some of its associated islands rather than with *D. peronii* from the Lesser Sunda Islands. The Sulawesian species differs most conspicuously from *peronii* in its lack of differentiation of the antero-internal corner of m$_1$ into a distinct cusp or small ledge, the inner or lingual ridge of the tooth being perfectly simple and lacking any notch or division. Andersen (1912) drew attention to a number of similarities between *exoleta* and *D. pannietensis* (De Vis, 1905) from the Trobriand Islands, which he thought differed from *exoleta* only in smaller size and in the lack of surface ridging on m$_1$, so considering the two taxa closely related. Later, Thomas (1914*a*) in describing *D. anderseni* remarked that this form from the islands of Manus and Ruk in the Bismarck Archipelago was intermediate in size between *exoleta* and *moluccensis*, an opinion confirmed to some extent by Bergmans (1979) who has examined specimens from a number of other islands in the Archipelago. As in *pannietensis* the dentition of *anderseni* is like that of *moluccensis*. Laurie & Hill (1954) recognised *exoleta* as a distinct species but listed both *pannietensis* and *anderseni* as subspecies of *D. moluccensis*. More recently, De Jong & Bergmans (1981) reviewed known specimens of *exoleta* in some detail and considered it to be a distinct species related in dental morphology to *chapmani* Rabor, 1952 from the Philippines, *moluccensis, anderseni* and *pannietensis*.

Bergmans (1975, 1978, 1979) has discussed and re-examined *pannietensis* and *anderseni*. He concluded (1975, 1979) that both should be considered specifically distinct on account of their smaller size when compared with *D. moluccensis moluccensis* and *D. m. magna* but it is not clear to what extent they differ from each other. This author (1975) suggested that to consider all of these conspecific involved the acceptance of an exceptional size range within one species, although (1979) he has himself accepted a considerable range of size among specimens from the islands (Louisiades, D'Entrecasteaux, Trobriand, Woodlark) immediately to the east of New Guinea that he considers all referable to *pannietensis*. Examination of the measurements provided by Bergmans (1979) suggests that some at least of the specimens that he refers to *pannietensis* are similar in size to *anderseni*: indeed, they overlap the measurements given by this author (1975, 1979) for the latter, although admittedly sexual differences in size may be involved. Moreover, Koopman (1979) in recording specimens from some of the small islands (Karkar, Bagabag, Umboi) off northeastern New Guinea and from the Bismarck Archipelago suggested that populations intermediate between *magna* and *anderseni* are to be found on Karkar and Umboi. This author has since (1982) discussed the question in some detail and while retaining *anderseni* as a subspecies of *D. moluccensis* considered *pannietensis* specifically valid, at least until the genus is fully revised. Insufficient specimens are available in London to determine the matter definitively, but for the present I am unconvinced that *anderseni* and *pannietensis* should be considered species distinct from *moluccensis*: Bergmans (1978) himself admits that both are more closely related to *moluccensis* than to other species of the genus.

Bergmans (1979) provided a brief discussion of *exoleta* and compared it with *D. moluccensis pannietensis*, drawing attention to a number of differences. Of these, the relatively narrower interorbital and postorbital regions of *exoleta* also separate it (in the limited sample available) from *D. m. anderseni*, *D. m. magna* and *D. m. moluccensis*. For the present, therefore, I retain it as a distinct species and agree with Andersen (1912) in regarding it as the Sulawesian representative of the *moluccensis* group. The species is known to occur (De Jong & Bergmans, 1981) on Sulawesi, on the Togian Islands (Malenge) in the Gulf of Gorantalo, and on Muna Island.

Dobsonia minor (Dobson, 1879)

Cephalotes minor Dobson (1878), 1879 : 875. Amberbaki, NW New Guinea.

Specimens examined. Papua New Guinea: ♀♀ BM(NH) 73.1971–1973 Rauit, 3° 36′ S, 142° 15′ E (in alcohol); BM(NH) 74.337–338 Near Rauit (skulls) (all coll. Aberdeen University Exploration Society Expedition to New Guinea, 1973).

Cynopterus brachyotis brachyotis (Muller, 1838)

Pachysoma brachyotis Muller, 1838 : 146. R Dewei, Borneo.

Specimens examined. Burma: 3 ♂♂, 4 ♀♀ BM(NH) 78.64–70, ♀♀ BM(NH) 78.151–153 British Embassy Residence Compound, Rangoon (in alcohol; coll. D. W. & G. Walton).

N Sumatra: ♂♂, ♀ BM(NH) 81.675–677 Bohorok R, near Bukit Lawang, Langkat Reserve, Gunung Leuser Reserve complex (in alcohol; coll. R. Aveling).

S Sumatra: ♂♂ BM(NH) 78.1114–1115 Banda hurip, Pulas District, S Lampong; (?), ♀ BM(NH) 78.1116–1117 Asahan, Jabung District, Lampong; ♀ BM(NH) 78.1118 Lebung Dadup, Asahan, Jabung District, Lampong; ♀ BM(NH) 78.1119 Sukaraja tiga, Sukadana District, Lampong; ♂ BM(NH) 78.1120 Pring Kumpul, Pring Sewn District, Lampong; ♂♂ BM(NH) 78.1122–1123 Air Nanigan, Pulau Penggung District (all skins, skulls; presented by Museum Zoologicum Bogoriense).

N Sulawesi; ♂ (?), (?) BM(NH) 78.968–970 Tangkopo Batuangus, near Bitung (in alcohol; coll. A. M. Jones).

C Sulawesi: (?) BM(NH) 79.2333–2337 Shore of Lake Matano, c. 5 km W of Soroako (in alcohol, very bad condition; coll. P. Holmes); 21 ♂♂ (2 yg.), 10♀♀, neonate BM(NH) 81.1006–1036, R Ranu, 1° 51′ S, 121° 30′ E: 2 ♂♂, 5 ♀♀ (2 yg.) BM(NH) 81.1037–1044 Ganda Ganda, 1° 57′ S, 121° 21′ E (all in alcohol; coll. B. H. Gaskell, 'Operation Drake').

Banggui Archipelago: ♂ BM(NH) 81.1045 Potil Besar I; ♂♂ BM(NH) 81.1046–1048 Kelara, Besar I (all in alcohol; coll. B. H. Gaskell, 'Operation Drake').

Remarks. Although *C. brachyotis* is a relatively commonly collected bat in southeastern Asia these specimens are of especial interest since those from Rangoon appear to be the first recorded from Burma and the furthest west the species has been reported on the Asian mainland while there have been few previous records from Sumatra and Sulawesi. Specimens of *C. brachyotis* from southern Sumatra are from an area that proves to be of particular taxonomic interest when the status of its congeners *sphinx* and *titthaecheileus* is considered. In size all of these specimens agree well with the extensive representation of *C. b. brachyotis* in the British Museum (Natural History) which suggests a range of forearm length of 57–66 for this subspecies over its range from Burma and Indochina to Sumatra and Sulawesi. Specimens from southern Sumatra with length of forearm 61·0–65·7 and m^1–m^1 (crowns) 8·2–9·0 approach the weakly defined subspecies *C. b. javanicus* Andersen, 1910 from Java but fall within the limits given by this author for *C. b. brachyotis*.

DISCUSSION. *Cynopterus minor* Revilliod, 1911. The status of this nominal taxon must remain uncertain for the present. It is known so far apparently only from the holotype from Lambuja, SE Sulawesi, a small individual with a forearm length of 53 that may be a young adult or unusually small example of *C. brachyotis*. It seems unlikely, however, that Revilliod should fail to recognise it as such.

In addition the name *minor* poses an involved nomenclatorial problem. It was proposed by Lyon in 1908 as *Niadius minor* for the taxon subsequently recognised as the Sumatran representative of *Cynopterus horsfieldi* by Andersen (1912) who considered *Niadius* Miller, 1906 a synonym of *Cynopterus*. As a result, Andersen (1912 : 827) regarded *Cynopterus horsfieldi minor* (Lyon, 1908) to be preoccupied by the combination *Cynopterus (Cynonycteris) minor* used by Trouessart (1878) for the species otherwise known as *Rousettus minor* (Dobson, 1873*a,b*), as it is today. In rejecting *minor* of Lyon, 1908 on this account Andersen proposed *Cynopterus horsfieldi lyoni* in its place, a substitute that subsequently (Robinson & Kloss, 1918, 1919; Chasen, 1940) came into use. Hill (1961*a*) reviewed the circumstances surrounding this situation and on the basis of verbal advice in 1960 from the International Commission for Zoological Nomenclature that secondary homonyms are not to be permanently rejected concluded that since *Cynopterus (Cynonycteris) minor* as used by Trouessart referred to a *Rousettus* the name *minor* as proposed by Lyon in 1908 should become again the valid subspecific epithet for the Horsfield fruit bat of Sumatra and Malaya.

However, the current International Code of Zoological Nomenclature provides (Art. 59, (b), (i)) that a junior secondary homonym rejected before 1961 is permanently rejected and cannot be restored unless the employment of the replacement name is contrary to existing usage. Thus *Cynopterus horsfieldi lyoni* Andersen, 1912 must become the valid name for the Sumatran and Malayan representatives of *C. horsfieldi*. At the same time the Code (Art. 59, (b), (ii)) states that if the secondary homonymy has been overlooked or the junior name not replaced, and the taxa in question are no longer congeneric, the junior name is not to be rejected, even though one name was originally proposed in the current genus of the other. Therefore *Cynopterus minor* Revilliod, 1911, having by these rulings no competitor within *Cynopterus* (*minor* of Lyon, 1908 having been rejected and replaced by *lyoni* of Andersen, 1912) remains a valid name in this genus, and is unaffected by the combination *Cynopterus (Cynonycteris) minor* used by Trouessart (1878).

Cynopterus sphinx angulatus Miller, 1898

Cynopterus angulatus Miller, 1898 : 316. Trang, S Thailand.

SPECIMENS EXAMINED. S Sumatra: ♀♀ BM(NH) 78.1112–1113 Wai Miring, Kota Agung District, Lampong; ♂ BM(NH) 78.1121 Pring Kumpul, Pring Sewn District, Lampong; 5♂♂, 2 ♀♀ BM(NH) 78.1124–1130 Air Naningan, Pulau Panggung District (all skins, skulls; presented by Museum Zoologicum Bogoriense).

Krakatau 1, 6° 10′ S, 105° 26′ E: ♂ BM(NH) 74.240 (in alcohol, skull extracted; coll. G. Lincoln).

REMARKS. Hill & Thonglongya (1972) discussed the affinities of *angulatus* and considered it to be a subspecies of *C. sphinx* (Vahl, 1797) rather than of *C. brachyotis* with which (after Andersen, 1912) it had been previously associated by the majority of authors. According to Andersen (loc. cit.) *angulatus* occurs as far to the northwest as northern Burma and Assam: however, a much wider representation of *C. sphinx* from Burma and Thailand than was available to Andersen suggests that Burmese specimens (length of forearm (24) 68·3–74·5) should be referred to the larger *C. s. sphinx* and that those from Thailand (length of forearm (12) 64·9–73·7) represent the slightly smaller *C. s. angulatus*. Dammerman (1938) records specimens from Krakatau Island and from the nearby island of Verlaten as *angulatus*, with which their size (length of forearm 69–72, greatest length of skull 30·3–33·2, c–m^1 10–11·2) clearly associates them. These islands apparently lie at the known limit of the southeastern extension of *C. sphinx* as it is understood here. A single specimen (BM(NH) 23.10.7.22) from the island of Simalur, off the northwest coast of Sumatra is not *angulatus* as Thomas (1923*b*) recorded it but is an example of *C. horsfieldi* (Gray, 1843).

(?) Cynopterus sphinx pagensis Miller, 1906

Cynopterus pagensis Miller, 1906*b*: 62 North Pagi I, Mentawei Is.

SECIMENS EXAMINED. Siberut I, Mentawei Is: 2 ♂♂ (1 yg.) 2 ♀♀ BM(NH) 78.2914–2918 Base of Teitei Bulak, Sabeuleleu, Paitan R, off Saibi R; ♂ BM(NH) 78.2919 Near Tolailai, off Paitan R; ♂ BM(NH) 78.2920 Near Sibosua R, off Paitan R (all in alcohol, skulls of BM(NH) 78.2915–2920 extracted; coll. J. J. Whitten).

REMARKS. Specimens from Siberut Island average slightly larger in some respects (Table 2) than those from Sumatra. They may represent *pagensis*, which was synonymised with *angulatus* by Andersen (1912) but listed as a valid subspecies (of *C. brachyotis*) by Chasen (1940) (who included Siberut and Sipora I in the range of *pagensis*) on account of its apparently short ears when compared with *angulatus* and similarly retained by Tate (1942*c*) on grounds of darker colour. Two (BM(NH) 95.1.9.3–4) from Sipora were thought representative of *pagensis* by Andersen (loc. cit.) and are similar to those from Siberut. The Siberut specimens have relatively short ears (16·1–17·8) while the ears of the two from Sipora are rather longer (18·2–19·0). If this material in fact represents *pagensis* then as Andersen suggested this taxon is very close to *angulatus*. Specimens of *C. sphinx* from Krakatau and Verlaten Island also seem slightly larger than many Sumatran examples, but the sample size is small.

Cynopterus titthaecheileus titthaecheileus (Temminck, 1825)

Pteropus titthaecheileus Temminck, 1825 : 198, pl. 15, figs. 17, 19, 20. Buitenzorg, Java.

SPECIMENS EXAMINED. S Sumatra: ♂, ♀ BM(NH) 78.1106–1107 Bandan harip, Palas District, S Lampong; ♂ BM(NH) 78.1108 Relung Lelok, Natar District, S Lampong; ♂ BM(NH) 78.1109 Pring kumpul, Pring Sewn District, S Lampong; ♀ BM(NH) 78.1110 Air Naningan, Pulau Panggung District, Lampong; ♂ BM(NH) 78.1111 Gisting, Talang Padang District, Lampong (all skins, skulls; presented by Museum Zoologicum Bogoriense).

Krakatau I, 6° 10′ S, 105° 26′ E: ♀, 2 ♂♂ (1 imm.) BM(NH) 74.237–239 (in alcohol, skulls of BM(NH) 74.237–238 extracted; coll. G. Lincoln).

REMARKS. Specimens of *Cynopterus* here reported from S Sumatra and from Krakatoa are of considerable taxonomic interest. They fall clearly (in part from Krakatoa) into separate sympatric or near sympatric groups, corresponding to the taxa identified by Andersen (1912) as *brachyotis*, *angulatus* and *titthaecheileus*. Those of *titthaecheileus* from S Sumatra and Krakatoa average slightly smaller in some respects (Table 2) than *titthaecheileus* from Java but the differences are slight. They can be readily distinguished from *C. sphinx angulatus* (with which in three instances recorded here they occur) by their considerably larger size, relatively longer rostrum which is less markedly concave in dorsal profile, curving down less abruptly from the braincase, and their heavier canines. In turn *angulatus* although less characteristically larger than *brachyotis* (also recorded here sympatrically or nearly so with the other two taxa) has when compared with this smallest of the three forms a more rectangular, less tapered and more robust rostrum, with a longer palate that is generally wider, especially anteriorly, and larger, heavier cheekteeth. These three taxa I recognise as distinct species, namely *C. brachyotis (brachyotis)*, *C. sphinx (angulatus)* and *C. titthaecheileus (titthaecheileus)*.

Andersen (1912) recorded both *C. brachyotis brachyotis* and *C. sphinx angulatus* from Krapoh, Deli-Bedagei in northeastern Sumatra but although this author also recorded *C. titthaecheileus* from Sumatra he had no sympatric occurrence of this large bat with either of

Table 2 Measurements of *Cynopterus* from south Sumatra, Siberut Island, and Krakatoa (numbers of specimens examined in parentheses).

	C. b. brachyotis S Sumatra	*C. s. angulatus* S Sumatra	*C, s,* (?) *pagensis* Siberut I	*C.* *titthaecheileus* S Sumatra	*C. s.* *angulatus* ♂♂ Krakatoa I	*C.* *titthaecheileus* ♂, ♀ Krakatoa I
Length of forearm	(9) 55·6–65·2	(10) 64·8–70·1	(5) 66·3–72·4	(6) 73·1–81·0	68·7, 68·2	75·1. 75·4
Condylobasal length	(8) 26·4–28·5	(10) 30·1–32·0	(3) 31·0–32·1	(6) 33·1–34·8	29·0, 30·0	34·3. 33·8
Condylocanine length	(9) 26·0–27·9	(10) 28·4–30·6	(3) 30·1–31·5	(6) 32·3–34·0	28·3, 29·4	33·5, 32·9
Palatal length	(8) 13·8–15·4	(10) 15·6–16·7	(4) 16·2–17·5	(6) 17·5–19·0	15·9, 16·6	18·9, 18·1
Least interorbital width	(9) 5·8–6·6	(10) 6·4–6·9	(4) 6·6–6·8	(6) 6·3–6·8	6·2, 6·9	6·4, 6·6
Least postorbital width	(9) 5·9–6·8	(10) 6·1–7·6	(4) 6·6–7·2	(6) 5·8–6·6	6·3, 6·8	6·8, 5·7
Zygomatic width	(9) 18·1–19·9	(10) 19·5–21·1	(4) 19·9–21·9	(6) 20·9–23·8	19·4, 20·4	22·3, 22·1
Width of braincase	(9) 11·7–13·0	(10) 12·7–13·8	(4) 12·8–13·4	(6) 13·6–14·9	12·7, 12·9	14·3, 13·9
c^1–c^1 (alveoli)	(9) 5·8–6·3	(10) 6·3–7·0	(4) 6·2–7·0	(6) 7·2–7·8	6·6, 6·8	7·3, 7·3
pm^4–pm^4 (alveoli)	(9) 7·3–8·0	(10) 8·1–8·7	(4) 8·1–8·5	(6) 9·0–9·6	8·0, 8·4	9·3, 9·3
m^1–m^1 (crowns)	(9) 8·3–9·3	(8) 9·3–10·1	(4) 9·0–10·0	(6) 10·3–11·6	9·1, 9·5	10·5, 10·8
m^1–m^1 (alveoli)	(9) 8·0–8·9	(9) 8·8–9·9	(4) 9·0–9·8	(6) 9·9–11·5	9·0, 9·4	10·5, 10·6
c–m^2	(9) 9·0–10·2	(9) 9·9–10·8	(4) 10·3–11·4	(6) 11·4–12·5	10·6, 11·1	12·2, 11·8
Length complete mandible from condyles	(9) 19·5–21·9	(10) 21·7–23·0	(3) 23·4–24·5	(6) 25·2–27·0	22·3, 22·4	25·9, 25·8
Length right ramus from condyle	(9) 20·5–22·7	(10) 22·7–23·9	(3) 24·1–25·5	(6) 25·9–28·4	23·3, 23·9	27·0, 27·0
c–m_3	(9) 10·0–11·7	(9) 11·2–11·8	(4) 11·6–12·5	(6) 12·9–13·7	11·6, 11·9	13·4, 13·4

the other two species. Dammerman (1938) while reporting *C. sphinx angulatus* from Krakatoa and Verlaten I also recorded a specimen of *C. titthaecheileus* from the nearby island of Sebesi.

DISCUSSION. Andersen (1912) associated *titthaecheileus* with *C. sphinx* as a subspecies, notwithstanding that his arrangement of this part of the genus involved a wide geographical hiatus between *C. s. sphinx* in India, Burma and northern Thailand and '*C. s. titthaecheileus*' in Sumatra and Java. This author considered *angulatus,* which fills this gap, to be a subspecies of *C. brachyotis,* a circumstance leading him to the conclusion that sympatric subspecies of *C. brachyotis* of different geographic origins, namely *C. b. brachyotis* and *C. b. angulatus* were to be found in the Malay Peninsula and in Sumatra. Although initially challenged by other authors, notably by Kloss and by his colleague Robinson (Kloss, 1911, 1916, 1917, 1919, Andersen & Kloss, 1915, Robinson & Kloss, 1915*a*, 1915*b*, 1918) who thought that *angulatus* might more properly be considered a subspecies of *C. sphinx,* this concept prevailed until quite recently.

Chasen (1940) attempted to resolve the distributional dilemma created by Andersen by limiting *C. b. brachyotis* to Malaya, Sumatra, Borneo and some of the associated islands, *C. b. angulatus* to southern Thailand and its coastal islands, and to the Natuna and Anamba Islands. Thus this author envisaged a large form in the north of the Malay Peninsula, a smaller form occupying the rest of the area from northern Malaya to Borneo, Sumatra, and, as *C. b. javanicus* Andersen, 1910, to Java. Hill (1961*a*) followed the arrangement proposed by Chasen but pointed out that specimens in the British Museum (Natural History) indicated a much wider zone of intergradation in northern Malaya than Chasen envisaged. However, both views prove unacceptable since larger specimens with forearm 67·5–73 are found also in Sumatra and agree with the size range that Chasen gives for '*C. b. angulatus*', while small animals corresponding to *C. b. brachyotis* occur in Thailand (Hill & Thonglongya, 1972) and are here recorded as far west as Rangoon in Burma.

Hill & Thonglongya (1972) reviewed the history of *angulatus* and concluded from a study of the collections of the British Museum (Natural History) that little taxonomic significance could be given to the features used by Andersen (1912) to distinguish *C. sphinx* from '*C. brachyotis angulatus*', which he thought sympatric in Burma and northern Thailand. Consequently these authors regarded *angulatus* a subspecies of *C. sphinx*: indeed, specimens in London demonstrate that the large Indian *C. s. gangeticus* Andersen, 1910 and the slightly smaller *C. s. sphinx* from northeastern India and Burma merge in Burma and Thailand into the characteristically smaller *C. s. angulatus* which extends southward into the Malay Peninsula to Sumatra and possibly east to Borneo. Sody (1930) refers a specimen from Moerah Teweh, Montellat River, southeast central Borneo to *Cynopterus brachyotis angulatus*: his measurements, given in some detail because clearly he recognised the importance of the specimen agree closely with those of Sumatran examples ascribed to *C. sphinx angulatus,* of which there is as yet no published record from Java or from Sulawesi. The Sumatran and Javan *C. titthaecheileus* differs from both *C. sphinx sphinx* and *C. s. gangeticus* not only in its rather larger size, although large individuals of *gangeticus* are similar in size to the smallest of *titthaecheileus,* but also in having a much heavier, more robust skull with broader, higher and more substantial rostrum that is relatively longer. It differs similarly from *C. s. angulatus* but these distinguishing features are more pronounced when it is compared with this smaller form of *C. sphinx.*

Lack of material prevented Hill & Thonglongya (1972) from any detailed consideration of Sumatran *brachyotis, angulatus* and *titthaecheileus,* these authors following Andersen (1912) in treating the latter as a subspecies of *C. sphinx* and, by implication, regarding Sumatran specimens attributed to it as large examples of *C. s. angulatus.* Until recently, the collections in London contained only an immature skeleton from Sumatra referred to *titthaecheileus*: other early Sumatran records of this species apparently rest on Andersen (loc. cit.) who examined most, if not all of the specimens before then reported in the literature.

Cynopterus major Miller, 1960*b*, from Nias Island, off west Sumatra is listed by Chasen (1940) as a subspecies of *C. sphinx*. Its very large size (length of forearm 75·5–82·0) however, suggests that more probably it is a subspecies of *C. titthaecheileus*. Similarly, *C. sphinx terminus* Sody, 1940*b* from Timor is also a large form (length of forearm 75·2–83) but has a relatively compact skull (condylobasal length 30·2–32·2), with a stout but short rostrum (Sody, 1940*b*, Goodwin, 1979). On geographical grounds, however, it is more likely to represent *C. titthaecheileus*: its relatively small skull might well justify recognition as a distinct species.

The relevant species and subspecies of *Cynopterus* may be summarised:

Cynopterus brachyotis (Muller, 1838)	
C. b. ceylonensis Gray, 1870	Sri Lanka
C. b. brachysoma Dobson, 1871*a,c* (*andamanensis* Dobson, 1873*b*)	Andaman Is.
C. b. brachyotis (Muller, 1838)	S Burma to Vietnam, Malaya, Sumatra, Borneo and many small associated islands, Bawean I, Philippine Is, Talaud I, Sulawesi, Peleng I.
C. b. altitudinis Hill, 1961*a*	Malayan highlands.
C. b. minutus Miller, 1906*b*	Nias I, off W Sumatra.
C. b. concolor Sody, 1940*a*	Engano I, off W Sumatra
C. b. javanicus Andersen, 1910	Java, Madura I, Bali
C. b. insularum Andersen, 1910	Kangean I, Mata Siri I.
Cynopterus minor Revilliod, 1911	SE Sulawesi
Cynopterus archipelagus Taylor, 1934	Polillo I, Philippine Is.
Cynopterus sphinx (Vahl, 1797)	
C. s. gangeticus Andersen, 1910	C, NW India.
C. s. sphinx (Vahl, 1797)	Sri Lanka, peninsular and NE India, Burma
C. s. angulatus Miller, 1898	N Burma to S China, Hainan I, Vietnam, Langkawi I, N Malaya, Sumatra, Krakatoa I. Verlaten I, (?) Borneo.
C. s. scherzeri Zelebor, 1869	Car Nicobar I.
C. s. serasani Paradiso, 1971	Serasan I, Natuna Is.
C. s. babi Lyon, 1916	Babi I, near Simalur I, off W Sumatra.
(?) *C. s. pagensis* Miller, 1906*b*	Mentawei Is, off W Sumatra.
Cynopterus titthaecheileus (Temminck, 1825)	
C. t. titthaecheileus (Temminck, 1825)	Sumatra, Krakatoa I, Sebesi I, Java, Lombok I.
(?) *C. t. major* Miller, 1906*b*	Nias I, off W Sumatra.
(?) *Cynopterus terminus* Sody, 1940*b*	Timor I.

Megaerops (?) ecaudatus (Temminck, 1837)

Pachysoma ecaudatum Temminck, 1837 : 94. Padang, W Sumatra.

SPECIMEN EXAMINED. N India: ♀ BM(NH) 16.3.25.1 Pashok, Darjeeling, 3000 ft (skin, skull; coll. N. A. Baptista, Bombay Natural History Society's Mammal Survey of India, Burma and Ceylon).

REMARKS. This specimen is one of two originally reported from Pashok by Wroughton (1916) as *Cynopterus sphinx*, to which he referred two others from Tong Song, also in the vicinity of Darjeeling. There is no record of these three remaining specimens in the British Museum (Natural History) and they are presumably in the collections of the Bombay Natural History Society. A further specimen, BM(NH) 16.3.25.2 from Gopaldhara, 17 miles W of Sonada Railway Station, SW of Darjeeling is unreported by Wroughton and without doubt represents *Cynopterus sphinx*.

There is no previous published record of *Megaerops* from further west than northern Thailand, whence *M. ecaudatus* was reported by Hill & Thonglongya (1972), the species extending otherwise to Malaya, Sumatra and Borneo. This Indian example is similar in many features to specimens from Chiangmai, northern Thailand (♂ BM(NH) 70.1440) and Vietnam (BM(NH) 26.10.14.13) but its upper incisors, upper canines and anterior lower premolars (pm_2) are a little more massive. The narial branch of the premaxilla is less attenuated in its upper part but is equalled in this respect by specimens from Pahang, Malaya. Specimens from India, northern Thailand and Vietnam are slightly larger in some respects than those from Malaya but the differences are small and the number of examples limited.

Hill & Boeadi (1978) drew attention to variation in rostral profile and outline in *M. ecaudatus*, indicating that in specimens from Thailand and Vietnam the rostrum is slightly shorter and less elevated anteriorly than in Peninsular and Bornean examples, the rostral profile sloping more gradually to the tip. These authors also found variation in the degree of lateral compression of the rostrum. The specimens from northern India, northern Thailand and Vietnam have a short, broad rostrum that is not markedly concave frontally: others from southern Thailand, Malaya and Borneo have a slightly longer rostrum with a rather more abruptly concave profile, the rostrum sharply compressed laterally to give its upper part distinctly and strongly concave lateral margins. A series from Pahang, however, tends to some extent to bridge this difference, some specimens (for example ♀♀ BM(NH) 60.734, 60.736) having rostra that are a little less abruptly concave in profile and less laterally compressed than in more extreme Peninsular or Bornean examples. For these reasons northern specimens are referred to *M. ecaudatus* with some hesitation.

Measurements (♀ BM(NH) 16.3.25.1, ♂ BM(NH) 70.1440 from Doi Pahompok, Fang District, Chiangmai, N. Thailand, c. 18° 43′ N, 98° 59′ E and ♀ BM(NH) 26.10.4.13 from Dak-to, Annam, Vietnam, in that order); length of forearm 60·5, 55·7, 59·9; greatest length of skull to gnathion 27·4, 26·9, 28·2; condylobasal length 26·7, 25·6, 27·4; condylocanine length 26·6, 25·7, 27·2; length front of orbit–tip of nasals 6·9, 6·5, 7·1; palatal length 13·9, 13·3, 14·1; length palation–basion 10·8, 10·6, 11·1; median depth of premaxillae 1·4, 1·5, 1·4; rostral height at front of c^1 5·0, 4·7, 4·7; rostral height at centre of pm^3 6·5, 6·3, 6·0; lachrymal width 9·6, —, 9·8; least interorbital width 5·2, 5·5, 5·7; least postorbital width 5·3, 6·3, 6·0; zygomatic width 17·8, 18·5, —; width of braincase 12·1, 12·2, 12·3; mastoid width 11·6, 11·7, 11·8; orbital diameter 8·1, 8·0, 7·9; c^1–c^1 (crowns) 6·0, 5·4, 5·5, (alveoli), 5·5, 5·1, 5·3; m^1–m^1 (crowns) —, 8·6, 8·3, (alveoli) 8·3, 8·5, 8·4; c^1–c^1 (cingula, internally) 2·7, 2·8, 2·6; pm^4–pm^4 (crowns, externally) —, 8·8, 8·4, (internally) —, 5·9, 5·3; width of mesopterygoid fossa 4·2, 4·0, 4·2; c–m^1 (crowns) 8·6, 8·5, 8·9, (alveoli) 8·3, 8·1, 8·5; length complete mandible from condyles 19·9, 18·9, 19·7; length right ramus from condyle 20·6, 20·0, 20·7; c–m_2 (crowns) —, 9·4, 9·8, (alveoli) 9·5, 9·3, 9·6.

Measurements of selected teeth (BM(NH) 16.3.25.1, 70.1440, 26.10.4.13): length i^2 0·56, 0·48, 0·51; width i^2 0·58, 0·41, 0·44; length i^3 0·53, 0·46, 0·46; width i^3 0·45, 0·35, 0·43; length c^1 (from front face) 1·98, 1·71, 1·82; width c^1 1·67, 1·39, 1·52; length pm_2 0·71, 0·70, 0·61; width pm_2 1·02, 0·87, 0·80.

Chironax melanocephalus (Temminck, 1825)

Pteropus melanocephalus Temminck, 1825 : 190, pls. 12, 16, figs. 3, 4. Bantam, Java.

Specimens examined. N Sumatra: ♀♀ BM(NH) 81.678–679 Near Bukit Lawang, Bohorok R (Bohorok orang utan rehabilitation centre), Langkat Reserve, Gunung Leuser Reserve complex (in alcohol; coll. R. Aveling).

W Java: 3 ♂♂, 3 ♀♀ BM(NH) 78.1085–1088 (skins, skulls), BM(NH) 78.1089–1090 (in alcohol) Cibodas, Mt. Gede (presented by Museum Zoologicum Bogoriense).

Specimens reported but not examined. N Sulawesi: ♀♀ Zoologisch Museum, Amsterdam ZMA 21.638–639 Over an upper tributary of Sungei Mauk, Cagar Alam Dumoga, 960 m (in alcohol; coll. K. D. Bishop, F. G. Rozendaal and W. F. Rodenburg).

Remarks. There are relatively few references to this species in the literature and for many years it was known only from the original material from Java, in the Rijksmuseum van Naturrlijke Historie, Leiden (Andersen, 1912). Thomas (1923*a*) reported a specimen (BM(NH) 23.1.2.2, a juvenile) from Nias Island, off west Sumatra, Chasen (1940) subsequently recording specimens from northern Sumatra and from Selangor, Malaya. More recently further specimens have been reported from Selangor by Hill (1961*a*) and Hill & Thonglongya (1972) have recorded others from Pahang, Malaya and from Nakon Sri Thamrat in southern Thailand. Finally, Hill (1974) provisionally referred a young adult from Sulawesi to this species, which does not appear to have been reported from Java since originally described by Temminck. Moreover, none of the specimens subsequently recorded from other parts of the Malaysian region appear to have been compared directly with Javan material. The additional specimens reported here are of some interest since those from Java enable such a comparison to be made, not only with Malayan but also with Sumatran examples. Additionally, Dr. W. Bergmans has provided details and measurements of two specimens from Sulawesi in the Zoologisch Museum, Amsterdam that he has identified as *C. melanocephalus.*

Andersen (1912) found the two 'cotypes' in the Rijkmuseum van Natuurlijke Historie to be so faded as to be unsuitable for description. According to Temminck (1825) 'The hairs on the back are of two colours, a yellowish white at the base and an ashy black at the tip; nape, top of the head and muzzle black; the hairs diverging from a common centre on the sides of the neck, serving probably to conceal an apparatus that secretes an odorous fluid. All of the other parts beneath are a yellowish white and dull; membranes a dark brown.'

Specimens from Java agree closely in pelage colour with the description by Temminck. Dorsally the hairs are whitish or slightly yellowish white at the base and for much of their length, and are tipped with dark brown or blackish brown; the nape and the head are a darker, more blackish tint, while the underparts are dull greyish white, tinged with yellow. As Temminck remarked, there is a radial tuft of hairs at the side of the neck: these hairs are greyish white throughout their length and are a little coarser in texture than the surrounding pelage. The tuft itself is usually slightly more obvious in male than in female specimens. A male example (BM(NH) 67.1488) in dry preservation from Pahang, Malaya is very similar in overall coloration to Javan specimens but the neck tufts are orange, while a female (BM(NH) 70.1441) from southern Thailand has a slightly less blackish head and is browner ventrally, the neck tufts less prominent than in the male from Pahang (Hill & Thonglongya, 1972) and less distinctly orange. One of the two females (BM(NH) 81.679) recorded here from Sumatra has quite well marked orange neck tufts but the other example has no obvious neck patches. In both the throat is white or creamy white. Other specimens from Pahang (BM(NH) 67.1484–1486), Trengganu (BM(NH) 75.1233) and Selangor (BM(NH) 60.865–878) in Malaya, also preserved in alcohol, confirm that the neck tufts or patches are generally less developed in females and indicate that they are not invariably orange or tinged with orange although inevitably some changes in colour have occurred through prolonged immersion. The young adult female (BM(NH) 73.1802) from southern Sulawesi provisionally referred to *C. melanocephalus* by Hill (1974) is a little paler dorsally than Javan specimens and is tinged with grey over the shoulders: the nape and head are dark greyish brown rather than black, and it has prominent white neck patches, the white extending to the throat. According to Dr. Bergmans one of the Sulawesian specimens (ZMA 21.639) in Amsterdam agrees in colour with the description (Hill, 1974) of this specimen: the other (ZMA 21.638) is somewhat lighter on the head and back but may be subadult.

Wing indices (Table 3) for the Javan specimens are in broad agreement with those given by Andersen (1912) for the two 'cotypes' of *C. melanocephalus,* although not unexpectedly there is a greater variation in the lengths of the digital components than was found by this author in so limited a sample. The metacarpals of the third, fourth and fifth digits, the first and second phalanges of the third digit and the second phalanges of the fourth and fifth digits of examples from Java are generally relatively shorter than are those of specimens from Sumatra and from the Malayan mainland, the third metacarpal especially so. On the basis of the two 'cotypes' Andersen (loc. cit.) noted of the wing of *Chironax* when compared with that of the closely related genus *Balionycteris* that the metacarpals of the third, fourth and fifth digits were not lengthened (lengthened in *Balionycteris*) the second phalange of the third digit was subequal in length to its metacarpal (much shorter in *Balionycteris*) and that the second phalanges of the fourth and fifth digits were slightly but distinctly longer than the associated first phalanges of the same digits (shorter in *Balionycteris*). The Javan specimens tend to support these contentions: in Sumatran and Malayan specimens the metacarpals of the third, fourth and fifth digits are lengthened to approach the condition found in *Balionycteris* but the second phalange in each of these digits is also correspondingly lengthened to retain more or less the relative proportions of *Chironax.* Specimens from Sulawesi have similarly lengthened third, fourth and fifth metacarpals but the second phalange of the third, fourth digits and on occasion of the fifth digit is relatively shortened as in *Balionycteris.*

Cranially the Javan specimens are similar in structure and size to those from Malaya, with similar teeth, as have the specimens from Sumatra: the second upper premolar (pm^3) has a well-marked antero-external supplementary cusp and the third upper premolar (pm^4) is more or less rectangular as in Malayan specimens. The young adult (BM(NH) 73.1802 from Sulawesi thus differs from Javan examples in much the same ways as it was found to differ (Hill, 1974) from those from Malaya: in some respects the skull is a little smaller, its supraorbital region is slightly more swollen and the postorbital processes a little more massively developed, while pm^3 lacks a well developed antero-external supplementary cusp and pm^4 is more rounded, dental features in which it also differs from the Sumatran specimens. Two points not mentioned in the account of BM(NH) 73.1802 are that the rear edge of the bony post-palate is slightly concave rather than straight or nearly so as in Javan and Malayan examples, and that one of the inner lower incisors (i$_2$) is missing. Dr Bergmans remarks that in both Sulawesian examples in Amsterdam pm^3 also lacks an antero-external supplementary cusp: possibly this feature will be found to characterise the Sulawesian population.

External measurements of six specimens (except where indicated in parentheses) from Java (BM(NH) 78.1085–1090), with those of two (BM(NH) 81.678–679) from Sumatra: length of forearm 42·8–45·7, 41·9, 42·3; III^m 27·7–29·8, 28·9, 29·2; III^1 20·9–22·0, 21·0, 21·4; III^2 25·8–28·2, 25·2, 27·5; IV^m 26·5–28·2, 26·9, 27·3; IV^1 16·1–17·2, 16·4, 16·7; IV^2 17·1–18·9, 16·8, 18·2; V^m 27·8–29·5, 28·0, 28·1; V^1 14·0–14·9, 15·0, 14·5; V^2 15·1–16·0, 14·8, 15·9; length of ear from opening (2) 9·9, 10·5, 10·4, 10·9; greatest width of ear (2) 7·6, 7·8, 7·8, 7·3; length of tibia (2) 16·1, 16·2, 16·0, 15·9; length of foot (c.u.) (2) 10·5, 10·9, 9·5, 9·4.

Wing measurements (by Dr W. Bergmans) of two specimens (ZMA 21.638–639) from Sulawesi: length of forearm 45·6, 45·6; III^m 32·0, 32·4; III^1 23·1, 23·7; III^2 23·3, 26·8; IV^m 30·8, 31·0; IV^1 18·2, 17·9; IV^2 15·2, 17·1; V^m 32·6, 32·4; V^1 14·6, 15·3; V^2 13·8, 15·5.

Cranial measurements of four specimens (except where indicated in parentheses) from Java (BM(NH) 78.1085–1088): greatest length of skull 21·9–23·3; condylobasal length (3) 21·5–22·3; condylocanine length 21·0–22·0; length front of orbit–tip of nasals 5·0–5·5; length orbit–nares 5·1–5·6; palatal length (3) 10·4–11·7; length palation–incisive foramina (3) 8·6–10·0; length palation–basion (3) 8·1–8·7; lachrymal width 6·0–6·3; least interorbital width 4·3–4·4; least postorbital width 4·6–5·3; zygomatic width 14·5–14·8; width of braincase 9·8–10·2; mastoid width 10·0–10·5; orbital diameter 5·6–6·0; c^1–c^1 (crowns) (3)

Table 3 Wing indices (length of forearm = 1000) of *Chironax melanocephalus* and *Balionycteris maculata* (modified from Hill, 1974).

	Chironax melanocephalus										*Balionycteris maculata*
	Java			Sumatra		Malay Peninsula		Sulawesi			Malaya, Borneo
No. of specimens	1[1]	1[1]	6[2]	1[3]	1[4]	1[5]	16[6]	1[7]	1[8]	1[9]	20
III^{m}	639	633	634–652	688	690	680	678–711	704	702	711	708–780
III^{1}	488	489	472–490	501	502	474	488–532	507	507	520	473–547
III^{2}	639	622	575–625	607	652	584	583–658	568	511	588	559–652
IV^{m}	616	578	606–623	640	648	629	617–676	640	675	679	693–738
IV^{1}	372	378	361–401	391	396	373	357–414	373	399	393	374–430
IV^{2}	419	422	381–419	401	429	400	395–443	360	333	375	340–415
V^{m}	639	622	628–659	668	663	667	659–704	708	715	711	706–762
V^{1}	337	322	321–353	358	343	318	328–358	319	320	335	329–363
V^{2}	349	344	330–355	356	377	363	339–382	317	303	400	317–354

[1] 'Cotypes', from Andersen (1912); [2] BM(NH) 78.1085–1090; [3] BM(NH) 1981.678; [4] BM(NH) 1981.679; [5] BM(NH) 60.871, young adult; [6] BM(NH) 60.865–878 (in part), BM(NH) 67.1484–1486, BM(NH) 70.1441, BM(NH) 75.1233; [7] BM(NH) 73.1802, young adult; [8] ZMA 21.638; [9] ZMA 21.639.

4·4–4·5, (alveoli) (3) 4·1–4·2, (cingula, internally) (3) 1·9–2·2; pm^4–pm^4 (crowns) (3) 6·4–6·8, (alveoli) 6·1–6·6, (internally) (3) 3·8–4·1; m^1–m^1 (crowns) 6·1, 6·5, (alveoli) 6·1–6·4; width mesopterygoid fossa 3·1–3·3; c–m^1 (crowns) (3) 6·6–7·3; length complete mandible from condyles 15·1–16·3; length right ramus from condyle 16·1–17·2; coronoid height 7·6–8·7; c–m_2 (crowns) 7·5–7·9.

Thoopterus nigrescens (Gray, 1870)

Cynopterus marginatus var. *nigrescens* Gray, 1870 : 123. Morty (= Morotai) Island.
Cynopterus latidens Dobson, 1878 : 86. Morty (= Morotai) Island.

SPECIMENS EXAMINED. C Sulawesi: ♀, 2 ♂♂ BM(NH) 81.1049–1051 R Ranu, 1° 51′ S, 122° 22′ E; 8 ♂♂, 6 ♀♀ BM(NH) 81.1052–1065 Tambusisi Damar, Mt. 4000 ft. 1° 39′ S, 121° 22′ E (in alcohol. BM(NH) 81.1054, 81.1056, 81.1058–1061, 81.1063–1064 heads only; coll. B. H. Gaskell, 'Operation Drake').

REMARKS. There are few records of this long-haired cynopterine fruit bat which is known so far with certainty from Morotai Island and from Menado and Minahassa in northern Sulawesi. Its reported occurrence on Luzon Island in the Philippines is thought doubtful by Taylor (1934) although it may extend to the southernmost of these islands. Length of forearm in four examples 76·5–78·9.

DISCUSSION. This large bat is similar in many respects to the relatively recently described genus *Latidens* Thonglongya, 1972 from southern India, which is almost identical in external form and colour and has a similarly long, strong rostrum. Dentally, however, *Latidens* approaches the Malaysian genus *Penthetor,* differing in the outline of m^1, which is more or less square and not wedge-shaped, and in the wider, rather more square outline of pm_4 and m_1. The latter teeth, however, also have a low surface cusp and in this respect approach *Thoopterus.* These and other features suggest that *Thoopterus* is represented in Malaysia by *Penthetor* as was thought by Andersen (1912) and in southern India by *Latidens.* The three genera can be readily distinguished from each other by the incisive dentition, *Thoopterus* having incisors $\frac{2}{2}-\frac{2}{2}$, *Penthetor* $\frac{2}{1}-\frac{2}{1}$, and *Latidens* $\frac{1}{1}-\frac{1}{1}$.

Aethalops alecto (Thomas, 1923)

Aethalodes alecto Thomas, 1923*a* : 251. Indrapura Peak, Sumatra, 7300 ft.

SPECIMENS EXAMINED. W Java: ♂, ♀ BM(NH) 75.590–591 Cibodas, Mt. Gede, 1450 m, c. 6° 50′ S, 106° 44′ E (skins, skulls; presented Museum Zoologicum Bogoriense).

REMARKS. Two subspecies of the small fruit bat *A. alecto* are recognised, *A. a. alecto* from the Malayan mainland and from Sumatra, and *A. a. aequalis* Allen, 1938*a* from Sabah and Sarawak. Their diagnostic characters are reviewed in part by Hill (1961*a*, 1966*a*), who also gave measurements. The species has not been formally recorded hitherto from Java but that island is included within its distribution by Honacki *et al.* (1982). These specimens cannot be referred definitively to either of the described subspecies. They are similar in most respects to *A. a. alecto* but have longer forearms and longer and more massive incisors, with the anterior lower premolar (pm_2) larger (about twice the crown area of the lower incisor (i_2) against one and one half times the crown area of i_2 in *A. a. alecto*) and more substantial. They differ more noticeably from *A. a. aequalis* in rather longer forearms, longer skull and toothrows, in slightly heavier incisors, with the inner upper incisors (i^2) distinctly shorter than the outer tooth (i^3), in having the lower canine rounded antero-internally, not especially flattened, in larger anterior premolars (pm^2_2) with pm_2 in particular more massive (in *A. a. aequalis* it is about equal in crown area to i_2), the second premolars (pm^3_3) less closely approximated to the canines, pm^3 having a well developed anterior secondary basal cusp while pm_3 is rounded anteriorly, lacking any projecting vertical anterior ridge.

Measurements (BM(NH) 75.590, 75.591): length of forearm 50·3, 51·0; greatest length of skull —, 25·4; condylobasal length —, 24·8; condylocanine length —, 24·5; palatal length 13·3, 13·2; lachrymal width 6·8, 6·3; least interorbital width 5·4, 5·1; least postorbital width 5·6, 5·3; zygomatic width 16·1, 15·5; width of braincase 11·0, 10·2; mastoid width 11·6, 10·5; c^1–c^1 (crowns) 5·4, 5·1, (alveoli) 4·9, 4·5; pm^4–pm^4 (crowns) 8·0, 7·4, (alveoli) 7·5, 7·0; c–m^1 (crowns) 8·5, 8·1, (alveoli) 8·0, 7·7; length complete mandible from condyles 18·6, 18·2; length right ramus from condyle 19·4, 18·8; c–m_2 (crowns) 9·3, 8·8, (alveoli) 9·0, 8·6.

Javan specimens of *A. alecto* are clearly closely related to *A. a. alecto* from Malaya and Sumatra, (whence only the holotype appears to have been recorded) differing only in slightly greater size in some respects, in the greater length and size of the incisive dentition and in larger pm_2. The Bornean *A. a. aequalis* differs more from either *A. a. alecto* or from the Javan examples than these populations do from each other. It has long upper incisors (similar to those of the Javan specimens although slightly smaller) but i^2 is equal or nearly equal in length to i^3, the inner face of the lower canine opposite the incisor is flattened or even broadly but shallowly grooved, pm^3 lacks any well developed anterior secondary basal cusp and the anterior face of pm_3 is narrowly ridged from the cingulum to the tip of the tooth. For the present the subspecific designation of the Javanese specimens is left undecided, pending more material to establish clearly the limits of their variation.

Aethalops alecto aequalis Allen, 1938

Aethalops aequalis Allen, 1938 : 497. Lumu Lumu, Mt. Kinabalu, Sabah, 5500 ft.

Specimens examined. Sarawak, Borneo: ♀♀ BM(NH) 78.590–591 Camp 2, Gunung Mulu, Melinau, 3° 49′ N, 115° 50′ E, 550 m (in alcohol; obtained Earl of Cranbrook, Royal Geographical Society Expedition to Mulu, 1978).

Remarks. These specimens supplement earlier records of *A. a. aequalis* (summarised by Medway, 1977) all from the highlands of north and northeastern Borneo. They are, however, from a somewhat lower altitude than any previously obtained, the subspecies having not before been collected below some 3000 ft.

HARPYIONYCTERINAE

Harpyionycteris celebensis Miller & Hollister, 1921

Harpyionycteris celebensis Miller & Hollister, 1921 : 99. Gimpoe, C Sulawesi.

Specimens examined. C Sulawesi: 2 ♂♂, 5 ♀♀ (2 yg.) BM(NH) 81.1150–1156 R Ranu, 1° 51′ S, 121° 30′ E (in alcohol, skulls of BM(NH) 81.1150–1151, 81.1153, 81.1155 extracted); 2 ♂♂(1 yg.) BM(NH) 81.1157–1158 Tambusisi Damar, Mt. Tambusisi, c. 4000 ft, 1° 39′ S, 121° 23′ E (BM(NH) 81.1157 in alcohol, 81.1158 skull only) (all coll. B. H. Gaskell, 'Operation Drake').

Remarks. *Harpyionycteris celebensis* was said by Miller & Hollister (1921) to be like *H. whiteheadi* from the Philippine Islands but to have a conspicuous secondary cusp on each side (i.e. on the anterior and posterior faces) of the second upper premolar (pm^3) and to have molars with lower crowns and relatively higher cusps. Tate (1951) in a detailed evaluation of *Harpyionycteris* suggested that *celebensis* was probably no more than subspecifically related to *whiteheadi* but made no close comparison of their distinguishing features. This suggestion was adopted by Laurie & Hill (1954) who considered *Harpyionycteris* monotypic, *celebensis* being listed as a subspecies of *H. whiteheadi.*

More recently, Peterson & Fenton (1970) have reviewed the specimens then known of *Harpyionycteris,* considering *celebensis* to be a distinct species on account of its shorter, broader upper canine which is less proclivous than in *whiteheadi* and has a much wider posterior cusp when viewed laterally, and also to some extent in the presence in *celebensis* of a well developed secondary cusp on the posterior flange of pm^3. These authors apparently had available two adult examples from Sulawesi, one the holotype of *celebensis.* The series reported here from Sulawesi suggests that there is a considerable degree of variation in these features: variation in dental patterns in this genus can be quite extensive, as Peterson & Fenton pointed out in relation to the upper molars of the series from Negros Island, Philippine Islands that they described as *H. whiteheadi negrosensis.*

The series from Sulawesi consists of three subadult or young specimens and six adults. As in the series from Negros Island examined by Peterson & Fenton, immature specimens have a rather more strongly deflected braincase than do mature examples, and have a wider postorbital constriction. These authors also found the lower incisors generally absent from specimens of *H. whiteheadi* that they examined, three of twelve examples having only one incisor (on one side only) all of the others lacking lower incisors. Two immatures and two adults of the series from Sulawesi have two small, slightly spatulate lower incisors tightly sandwiched between the anterior part of the canine bases: one immature and two adults have one lower incisor, in one example (BM(NH) 81.1155) placed to one side with some indication that the corresponding tooth on the other side has been lost, in the others more centrally situated; and in two adults lower incisors are lacking.

The upper canines of specimens from Sulawesi are less proclivous and are generally rather more massive but shorter than those of the holotype of *H. whiteheadi* although in some the difference in size is small. The posterior canine cusp is variable in size: in a minority of specimens the cusp is large and massive, lacking any definite point, like that of the specimen (AMNH 153590) illustrated by Peterson & Fenton (1970), but more frequently the cusp is more or less triangular with a definite point, like that of the specimen photographed by Tate (1951, figs 1–3). Although generally larger than the corresponding cusp in the holotype of *H. whiteheadi* it may be on occasion similar in size to its counterpart in that species or even slightly smaller.

The cuspidation of pm^3 varies considerably in this series. The tooth in lateral profile ranges from a relatively high crowned structure with small but well developed supplementary cusps on its anterior and posterior margins extending along about three quarters the length of the tooth to just beneath the tip of the main cusp through stages in which the cusps are lower, about halfway along the length of the tooth, or present only anteriorly, the posterior cusp represented only by a flexure of the margin of the tooth, absent anteriorly but present posteriorly, or both effectively absent, their presence indicated only by a faint curvature of the edge of the main cusp. The tooth as a whole is lower than in the holotype of *H. whiteheadi,* although similar in overall bulk.

The molar teeth do not seem to be especially low crowned or high cusped in relation to those of *H. whiteheadi,* and there is no great degree of variation in their cuspidation such as that noted by Peterson & Fenton in the series that they named *H. whiteheadi negrosensis* from Negros Island. Cranially, specimens from Sulawesi have the median part of the palate more deeply excavated and transversely arched than does the holotype of *H. whiteheadi,* a feature not mentioned by Peterson & Fenton for the Sulawesian examples that they examined. Tate (1951) remarked that the yellowish markings on the wings of *H. whiteheadi* might be significant but similar yellowish spots or blotches are to be found on the wings of specimens from Sulawesi.

The palate ridges of Sulawesian specimens are similar to those of Philippine examples as illustrated by Sanborn (1952) and illustrated and described by Peterson & Fenton (1970). There are five anterior undivided ridges and three divided posterior ridges: these latter are greatly variable and the central ridge of the three is sometimes reduced to small paired raised swellings on each side of the median division, or tends to blend and merge with the first of the divided ridges. There is also an undivided ridge much more posteriorly situated near the rear edge of the palate.

External measurements of six adults: length of forearm 84·2–88·3; length of thumb (c. u.) 35·1–37·3; II^m 39·2–42·3; II^1 11·2–12·0; II^{2-3} (c. u.) 11·3–12·8; III^m 57·6–62·4; III^1 45·6–47·8; III^2 57·8–63·3; IV^m 54·0–58·5; IV^1 36·1–37·8; IV^2 35·3–37·5; V^m 55·9–58·3; V^1 28·9–31·3; V^2 32·7–35·7; length of tibia 29·2–29·5; length of foot (c.u.) 22·2–23·6.

Cranial measurements of four adults: greatest length of skull 41·2–42·0; condylobasal length 39·2–39·7; condylocanine length 39·0–39·6; length front of orbit–tip of nasals 10·4–11·5; palatal length 21·3–22·1; length of palation–incisive foramina 17·0–18·1; length palation–basion 15·7–16·4; lachrymal width 10·0–11·0; least interorbital width 6·4–7·0; least postorbital width 5·7–6·4; zygomatic width 23·4–24·1; width of braincase 15·7–16·7; height of braincase 13·3–14·3; mastoid width 14·6–15·6; orbital diameter 8·9–9·6; c^1–c^1 (crowns) 7·4–8·2, (alveoli) 6·8–7·4; (cingula, internally) 2·8–3·1; pm^3–pm^3 (crowns) 8·8–9·5; (alveoli) 8·3–9·1, (internally) 5·0–5·7; pm^4–pm^4 (crowns) 9·5–10·7, (alveoli) 9·1–10·3, (internally) 5·4–6·3; m^2–m^2 (crowns) 10·7–11·7, (alveoli) 10·6–11·6, (internally) 7·3–8·1; width mesopterygoid fossa 4·6–5·2; c–m^2 16·6–16·8; length complete mandible from condyles 31·5–32·3; length right ramus from condyle 32·4–33·9; depth mandible between pm_4 and m_1 4·0–4·5; depth mandible behind m_3 5·3–5·7; coronoid height 15·1–15·8; c–m_3 17·7–18·4.

DISCUSSION. Peterson & Fenton (1970) present a persuasive argument for the recognition of *celebensis* as a distinct species, supported by morphological features drawn from the skull and dentition, by zoogeographical argument based on the considerable distance over open water separating Sulawesi from the nearest small islands that might serve as stepping stones from the Philippines and the separation of these islands from Sulawesi by Wallace's Line. They also base their view on the fact that the genus has not been recorded from Borneo which is less widely separated from Sulawesi at its point of closest approach (in fact Borneo lies on the other side of Wallace's Line and is connected to the Philippine Islands by two chains of relatively narrowly separated islands) and on a presumed dietary specialisation limiting *Harpyionycteris* to high altitude species of fruit.

Certain of the morphological characters, however, are clearly valueless or perhaps are unreliable for diagnostic purposes. The presence or absence of an accessory posterior cusp on the second upper premolar (pm^3) evidently lacks taxonomic reliability and the dimensions and form of the accessory canine cusp do not seem firm characters on which diagnosis can be based. The degree of proclivity of the upper canine may also prove unreliable: although in *celebensis* the upper canines are generally less proclivous than in *whiteheadi* the figure by Peterson & Fenton (1970, fig. 6) indicates that the upper canines of the subspecies *H. whiteheadi negrosensis* are nearer in proclivity to those of *celebensis* than to those of *H. w. whiteheadi*. According to Peterson & Fenton (1970) no more than three examples of this latter subspecies are known and of these only the holotype has been available for comparison: this suggests that *celebensis* differs from *H. w. whiteheadi* in its generally less forwardly projecting upper canines which are usually shorter and anteroposteriorly a little broader, and in a rather more deeply excavated median palate.

The zoogeographical case put forward by Peterson & Fenton (1970) also deserves further consideration. Apart from *Harpyionycteris* only *Acerodon, Dobsonia* and *Nyctimene* among other fruit bats are known so far to bridge the water gap between Sulawesi and the Philippine Islands yet apparently do not occur in Borneo. The large *Acerodon* occurs also on the Talaud Islands, and *Dobsonia* has one form, *chapmani*, on Negros Island (where *Harpyionycteris* is also found) apparently related to a predominantly Moluccan and New Guinea species, *D. moluccensis*. The genus *Nyctimene* has also been reported from Negros Island (Rabor *et al.*, 1970). The distribution pattern is clearly an unusual one for fruit bats and possibly as Peterson & Fenton suggest the Sulawesian population of *Harpyionycteris* may have been long isolated. On the other hand, Sulawesian specimens from R Ranu show that *Harpyionycteris* is not exclusively a high altitude bat, although in Sulawesi it was also obtained at a considerable altitude on Mount Tambusisi, and not necessarily dependent on high altitude species of fruit that might not be available on small islands. It is probably correct to say as Peterson & Fenton (1970) do that it is a specialised feeder: its multicuspid teeth suggest a diet of hard fruit.

In view of these various considerations, for the present I also regard *celebensis* as specifically distinct from *H. whiteheadi,* but with strong reservations that this view may well be modified when fully adequate comparative material is available. In particular, further specimens of *H. whiteheadi whiteheadi* are required to establish the extent of dental variation in this subspecies, if any. It also seems possible that the distribution of *Harpyionycteris* is imperfectly known as yet, and that it may be found to occur at least on some of the other islands that abound in the Philippine and Sulawesian regions. Such additional material might prove highly relevant to any further consideration of the relative status of the two taxa.

NYCTIMENINAE

Nyctimene albiventer papuanus Andersen, 1910

Nyctimene papuanus Andersen, 1910 : 621. Milne Bay, Papua New Guinea.

SPECIMENS EXAMINED. Papua New Guinea: ♂ BM(NH) 69.1417 Olsobip, Upper Fly R, 1500–2000 ft (skin, skull; coll. J. I. Menzies); ♀♀BM(NH) 73.2106–2025 Kairiru ridge, centre of Kairiru I, near Wewak, East Sepik, c. 2000 ft (in alcohol; coll. Aberdeen University Exploration Society Expedition to New Guinea, 1973); ♀ BM(NH) 78.867 Sapi Creek Forest Reserve, near Baku, Gogol Valley, Madang, c. 40 m (in alcohol), ♀ BM(NH) 78.868 Sapi Creek, c. 8 km E of Baku (skin, skull) (both coll. P. A. Morris); ♂ BM(NH) 80.565 Lobota Cave, Morobe, 7° 15′ S, 147° 09′ E, 18 ♂♂, 11 ♀♀ BM(NH) 80.566–594 Buso, Morobe, 7° 17′ S, 147° 08′ E (all in alcohol; coll. B. H. Gaskell, 'Operation Drake').

Nyctimene cephalotes cephalotes (Pallas, 1767)

Vespertilio cephalotes Pallas, 1767 : 10, pls. 1, 2. 'Moluccas'. Type locality fixed on Amboina I by Andersen (1912).

SPECIMENS EXAMINED. Molucca Is: ♂, ♀, ♂ BM(NH) 81.1128–1130 Kaiteto, Amboina I (in alcohol; coll. B. H. Gaskell, 'Operation Drake').

C Sulawesi: 14♂♂, 4 ♀♀ BM(NH) 81.1131–1148 R Ranu, 1° 51′ S, 121° 30′ E (in alcohol; coll. B. H. Gaskell, 'Operation Drake').

Nyctimene major lullulae Thomas, 1904

Nyctimene major lullulae Thomas, 1904 : 197. Woodlark I, Trobriand Is.

SPECIMENS EXAMINED. Papua New Guinea: ♂♂ BM(NH) 75.1861–1862 Kadovar I, Schouten Is, 3° 38 S, 144° 36′ E (in alcohol; coll. A. M. Jones, Aberdeen University Exploration Society).

REMARKS. In overall size (length of forearm 69·9, 67·5; m^1–m^1 (crowns) 9·8, 9·9; (alveoli) 9·6, 9·7; c–m^1 12·0, 11·9) and in the size of their teeth these specimens generally approach more closely to *N. m. lullulae* than to either of the other subspecies known from the islands surrounding the northeastern and eastern coasts of New Guinea, namely *N. m. major* (Dobson, 1877*a*) from the Bismarck Archipelago and *N. m. geminus* Andersen, 1910 from eastern New Guinea and its associated islands.

DISCUSSION. Koopman (1979) has discussed the distribution of *N. major* on the islands off northeastern New Guinea in some detail. This author found that while the larger subspecies *N. m. major* occurred on the more outlying islands of the Bismarck Archipelago, smaller specimens from the inshore islands of Karkar and Bagabag are similar in size to *N. m. lullulae* from the more easterly island of Woodlark. Kadovar Island lies considerably to the northwest of Karkar and Bagabag and is evidently occupied by a population of similar smaller overall size. More recently, Koopman (1982) has examined variation in this species on the islands off the eastern tip of New Guinea.

Nyctimene aello (Thomas, 1900)

Cephalotes aello Thomas, 1900 : 216. Milne Bay, Papua New Guinea.

SPECIMENS EXAMINED. Papua New Guinea: ♂, (?) BM(NH) 68.1109–1110 Laloki, 9° 26′ S, 147° 20′ E (skins, skulls; coll. J. I. Menzies); ♂, ♀ BM(NH) 73.2031–2032 Victoria Bay, NW end of Kairiru I, near Wewak, East Sepik; ♂, ♀ BM(NH) 73.2033–2034 Sabor Kunai, E end of Kairiru I (all in alcohol; coll. Aberdeen University Exploration Society Expedition to New Guinea, 1973); 6 ♂♂, ♀ BM(NH) 80.595–601 Buso, Morobe, 7° 17′ S, 147° 08′ E (in alcohol; coll. B. H. Gaskell, 'Operation Drake').

REMARKS. Specimens in dry preservation from Laloki are pale brown dorsally and have a broad black dorsal stripe extending almost to the head: one is fulvous ventrally, the other more buffy brown, the flanks in both rather more brownish. Those from Kairiru and Buso are brownish dorsally, with a similar generally broad dorsal stripe: the throat, chest and centre of the belly is dull buffy white or buffy brown shading into brownish on the flanks. All, however, have been preserved in alcohol.

DISCUSSION. Laurie & Hill (1954) list *N. aello* with two subspecies, *N. a. aello* from eastern New Guinea and *N. a. celaeano* Thomas, 1922*a* & *b* from the western and northwestern parts of the island. According to Thomas (1922*a* & *b*) *celaeano* is slightly smaller than *aello* and is browner and less yellowish or fulvous, the dorsal surface less yellow and much of the ventral surface dull buffy white, the sides brown, not fulvous as in *aello*. These differences in colour between the holotypes of *celaeno* (BM(NH) 22.2.2.2) and *aello* (BM(NH) 99.12.3.1) are not entirely supported by the newly acquired material reported here or by other specimens in dry preservation in the collections of the British Museum (Natural History). The holotype of *celaeno* has the head, both above and below, the nape and the shoulders pale yellowish white, in contrast to the more fulvous coloration of the holotype of *aello*: the remainder of the dorsal surface is slightly paler than in *aello* and the ventral surface is dull buffy white, lacking the orange tinge characteristic of this specimen. A second specimen (BM(NH) 29.5.27.3) referred to *celaeno*, from Wasjor, West Irian almost exactly resembles the holotype of *aello* in coloration, corresponding closely in ventral colour to the more brightly coloured (BM(NH) 68.1110) of the two from Laloki. BM(NH) 1939.1351 from Tamata, Mambare River and BM(NH) 1939.1352 from Takar are a slightly paler brown dorsally than the holotype of *aello* and ventrally are less strongly tinged with fulvous or orange, corresponding to but a little brighter ventrally than the duller (BM(NH) 68.1109) of the two Laloki examples.

The coloration of the holotype of *celaeno* is characteristic of immersion in alcohol: Thomas (1922*b*) remarked 'Adult male, skinned out of spirit' and its original labels show that in fact it was collected in 1910 (not 1912 as stated by Thomas, 1922*b*). It may not have been prepared as a dry skin until 1921 or 1922. Careful examination shows that it does retain ventrally some trace of a brighter colour along the flanks, although much bleached. Moreover, there is little of this brighter ventral coloration in specimens of *aello* that although relatively recently collected have been preserved in alcohol. There is every indication, therefore that the colour of the holotype of *celaeno* is of limited value as a comparative feature.

However, there is a number of cranial and dental features by which the holotype of *celaeno* differs from *aello*. It has a much shorter, rather broader rostrum, wider interorbital and intertemporal areas, the frontal region is more elevated in contrast to the rather depressed frontal region of *aello* (commented upon by Thomas, 1922*b*), the supraorbital ridges are more swollen and inflated, and on the whole the teeth are generally smaller, the upper canines less obviously proclivous than in *aello*. For the present it seems more appropriate to consider it a distinct species allied to *N. aello,* at least until more specimens can be examined to establish its status: BM(NH) 29.5.27.3 from Wasjor, West Irian, hitherto referred to *celaeno,* agrees externally and cranially with *N. aello* to which it should be allocated. Tate (1942*c*) thought *celaeno* apparently closely allied to *N. major* from New Guinea and its associated islands but this species differs quite widely

Paranyctimene raptor Tate, 1942

Paranyctimene raptor Tate, 1942*a* : 1. Oroville Camp, Fly R, about 4 miles below mouth of Elavala R, Papua New Guinea.

SPECIMENS EXAMINED. (?) BM(NH) 68.1111, ♂ BM(NH) 69.317 Laloki, about 12 miles N of Port Moresby, 9° 26′ S, 147° 20′ E (skins, skulls; coll. J. I. Menzies); 2 ♂♂, 3 ♀♀ (1 yg.) BM(NH) 73.2024–2028 Rauit, West Sepik, 1750 ft, 3° 36′ S, 142° 15′ E; ♂ BM(NH) 73.2029 Biip, ½ mile SE of Rauit, 1650 ft; ♂, ♀ BM(NH) 73.2030, 73.2035 Rauit R, W of Rauit, 900 ft (all in alcohol; coll. Aberdeen University Exploration Society Expedition to New Guinea, 1973); ♀ BM(NH) 75.1860 Rauit, West Sepik (in alcohol; coll. A. M. Jones, Aberdeen University Exploration Society); ♀ BM(NH) 78.869 Baiyer R, c. 50 km NW of Mt. Hagen, Western Highlands; ♀ BM(NH) 78.870 Sapi Creek Forest Reserve, near Baku, Gogol Valley, Madang; ♂ BM(NH) 78.871 Baiyer R area, Western Highlands; ♂ BM(NH) 78.872 Mt Hagen (town), Western Highlands (all in alcohol; coll. P. A. Morris); 2 ♂♂, 2 ♀♀ BM(NH) 80.602–605 Buso, Morobe; ♀ BM(NH) 81.1149 Avi, Mt. Hagen, Western Highlands (all in alcohol; coll. B. H. Gaskell, 'Operation Drake').

REMARKS. Specimens BM(NH) 73.2024–2030, 73.2035 are those reported by Grieg-Smith (1975) as *Nyctimene draconilla* Thomas, 1922*b,* which is similar in size and coloration to *Paranyctimene raptor.* This author commented upon the wide range extension that they indicated for *draconilla* (considered a subspecies of *N. albiventer* (Gray, 1863) by Laurie & Hill, 1954) and on their sympatric occurrence with *N. albiventer,* suggesting therefore that *draconilla* should be considered a distinct species. However, Koopman (1979) has reported the sympatric occurrence of *N. albiventer papuanus* with *N. draconilla* on the Upper Fly River in Papua New Guinea, later (1982) confirming his identification of *draconilla* from this locality.

MACROGLOSSINAE

Eonycteris spelaea (?) glandifera Lawrence, 1939

Eonycteris spelaea glandifera Lawrence, 1939: 38. Montalban Caves, Rizal Province, Luzon, Philippine Is.

SPECIMENS EXAMINED. S Sulawesi: 2 ♀♀(1 yg.), ♂ BM(NH) 81.1110–1112 Lalonggasu Meeto (Tomba Watu Cave), 18 km from Kendari Central (in alcohol, skull of BM(NH) 81.1112 extracted; coll. B. H. Gaskell, 'Operation Drake').

REMARKS. These specimens have longer forearms and cranially are a little larger in some respects than examples from Burma, Thailand, Malaya, Sumatra and Borneo. Moreover, the rostrum is larger, more massive and less tapered than in specimens from more westerly localities. The teeth of the male example, especially the canines, are a little larger than those of the adult female. Measurements: length of forearm (♂ BM(NH) 81.1112, ♀ BM(NH) 81.1111) 76·2, 74·2; cranial dimensions (♂ BM(NH) 81.1112): greatest length of skull 35·8;

greatest length of skull to canine 34·1; condylobasal length 34·0; condylocanine length 32·1; basal length to canine 30·1; palatal length 18·5; least interorbital width 6·9; least postorbital width 7·3; zygomatic width 22·4; width of braincase 14·3; mastoid width 13·8; width across occipital crests 13·1; c^1–c^1 (alveoli) 7·5; m^1–m^1 (crowns) 9·2; (alveoli) 9·2; c–m^2 13·0; length complete mandible from condyles 26·1; length right ramus from condyle 27·0; c–m_3 14·2.

Discussion. As Goodwin (1979) has pointed out, lack of material has led to some uncertainty in the classification of this genus. Detailed studies of *Eonycteris* may be said to begin with Andersen (1912), who recognised three species, *E. spelaea* (Dobson, 1871*a* & *c*), widely distributed from Burma to Sumatra, Java, the larger *E. major* Andersen, 1910 from northern Borneo, and, more doubtfully, *E. rosenbergi* Jentink, 1889 from Sulawesi, considering the last to be perhaps an aberrant *spelaea*. Subsequently Miller (1913) described *E. robusta* from Luzon Island, Philippine Islands. Chasen (1931) reported *spelaea* from Borneo, while Taylor (1934) reported further specimens from Luzon as *robusta* and described a second species, *longicauda,* from that island. However, Lawrence (1939) pointed out that Taylor had applied *robusta* to a hitherto undescribed subspecies of *E. spelaea* for which she proposed the name *glandifera,* and that in describing *longicauda* Taylor had in fact renamed *robusta* of Miller. Lawrence also indicated that specimens from Sumatra had no consistent characters separating them from *E. s. glandifera,* although Andersen (1912) had earlier thought Sumatran *Eonycteris* to be the same as those from Burma.

Tate (1942*c*) discussed the genus in some detail, recognising (excluding *rosenbergi* from Sulawesi) *spelaea, major* and *robusta* as distinct species. He concluded that two subspecies of *E. spelaea* could be recognised: one, *E. s. spelaea* he thought to extend from Burma and Vietnam through Malaya and Sumatra to east (sic) and central Java and possibly to Borneo (cf. Chasen, 1931), the other, *E. s. glandifera* occurring in the Philippines, in Bali, perhaps in eastern (sic) Java and probably in Borneo. Tate tentatively referred specimens from Bali to *E. s. glandifera,* others from southern Sumatra emphatically to *E. s. spelaea* rather than to *glandifera* as was done by Lawrence. More recently, Goodwin (1979) has provided an account of a female specimen from Timor Island which on size and coloration also appears to represent *E. s. glandifera.* Like Andersen (1912), Tate (loc. cit.) thought *rosenbergi* from Sulawesi most probably based on an anomalous specimens of *spelaea.* He also suggested that *robusta* (=*longicauda*) represented the Bornean *major* in the Philippine Islands and greatly extended the range of the latter species by referring to it a specimen from North Pagi Island, in the Mentawei Islands off west Sumatra.

The larger size and strong rostrum of specimens from Sulawesi suggests that they too should be referred to *E. s. glandifera.* Moreover, the Sulawesian male has the distinct throat band of long, tawny hairs described by Lawrence in *glandifera* and noted also in specimens from Bali by Tate (1942*c*). However, this feature seems less exclusive than implied by Tate who found no indication of this throat colouring in males of *E. s. spelaea.* Male specimens from Sarawak in the collections of the British Museum (Natural History) have an ochraceous tawny or even russet throat band although in other respects they agree closely with *E. s. spelaea* from the Asian mainland that like those seen by Tate lack any such coloration.

The status of *Callinycteris rosenbergi* Jentink, 1889 (=*Eonycteris rosenbergi*) remains uncertain. It is known only from the immature holotype in the Rijksmuseum van Natuurlijke Historie, Leiden, re-described in some detail by Andersen (1912). According to this author *rosenbergi* differs from *E. spelaea* in the absence of the last lower molar (m_3) on each side of the jaw; as he points out, m_3 is occasionally missing at least from one side of the jaw in *E. spelaea.* Miller (1907) who had seen a photograph of the holotype remarked on its heavy dentition. It is possible therefore that it is a young adult example of *E. s. glandifera*: certainly the palate ridges as illustrated by Jentink are characteristically the same as those of *E. s. glandifera* from Sulawesi. If this proves to be so, then *rosenbergi* must replace *glandifera* as the earlier name. In discussing this question Tate (1942*c*) erroneously refers to *rosenbergi* as *bernsteini* (a name actually used in the hipposiderid genus *Coelops*), thus creating a nomen nudum.

Macroglossus minimus lagochilus Matschie, 1899

Macroglossus lagochilus Matschie, 1899 : 96. Buru I, Molucca Is.

Specimens examined. C Sulawesi: ♂ BM(NH) 81.1113 Ganda Ganda, 1°57′ S, 121°21′ E; 5 ♂♂, 5 ♀♀ BM(NH) 81.1114–1123 R Ranu, 1° 51′ S, 121° 21′ E; ♂, ♀ BM(NH) 81.1124–1125 Tambusisi Damar, Mt. Tambusisi, c. 4000 ft, 1° 39′ S, 121° 22′ E (in alcohol; coll. B. H. Gaskell, 'Operation Drake').

Remarks. Specimens from Sulawesi agree closely with those from the Molucca Islands and from Borneo. Length of forearm in thirteen examples 38·4–41·9.

Discussion. There is considerable taxonomic confusion in the genus *Macroglossus,* not least resulting from its treatment by Andersen (1911, 1912), and identification difficulties have until recently been common with specimens from the western part of its range in Malaysia, Sumatra and Java. Mr A. N. Start (in litt.) has examined and studied *Macroglossus* from this region, but his findings have yet to be published. In the meantime, however, his views have influenced Lekagul & McNeely (1977) and Medway (1978) (or indirectly Ziegler, 1982) but these authors give no justification for their adoption of combinations of names differing from the generally used classification of Andersen (1912).

Thomas (1889) first recognised the existence of two species of *Macroglossus* when examining specimens from Aola, Guadalcanal Island in the Solomon Islands. These he distinguished readily from others from Java by the presence of a deep internarial groove extending to the upper lip, much shorter face, i.e. rostrum, and smaller size, their forearm lengths ranging from 38–43 mm, while in the Javan specimens the length of the forearm ranged from 45–48 mm. These specimens from the Solomon Islands he wrongly called *M. australis* (actually *Syconycteris australis*): in fact, they represent the form called *M. lagochilus* by Andersen (1912). Those from Java Thomas called *M. minimus*: their size refers them undoubtedly to the form called *M. minimus sobrinus* by Andersen (1911, 1912).

Andersen (1911, 1912) reviewed the genus in considerable detail. Basing his conclusions on the directionality of the nares and the extent and depth of the internarial groove, this author recognised two species, *M. minimus,* Indo-Chinese and Indo-Malayan, and *M. lagochilus,* Austro-Malayan, but with no distributional overlap. According to Andersen, *minimus* extended eastward through Java to Madura and Kangean Islands, perhaps to Timor, while *lagochilus* extended westward to Borneo and the Philippine Islands. He also recognised the existence of two forms in Java, one smaller, with shorter rostrum, which he called *M. minimus minimus,* the other larger, with relatively longer rostrum, which he called *M. minimus sobrinus,* this latter subspecies ranging to Sumatra, the Malay Peninsula, Thailand, Burma and northeastern India. Specimens examined by Thomas (1889) clearly represent this form, against which he compared *lagochilus* from the Solomon Islands. It is also worth noting that many years earlier Temminck (1837) had remarked upon differences in muzzle length in *Macroglossus,* recording that specimens from Sumatra had excessively long muzzles; the muzzles of those from Java proved a little shorter and little different from the muzzles of specimens from Timor, while others from Amboina Island had remarkably short muzzles compared with those of Sumatran examples. Andersen (loc. cit.) regarded *M. minimus minimus* as Javan, with *M. m. sobrinus* extending westward from Java through Sumatra to the Asian mainland: he also thought that *M. m. minimus* might be found to occur on Sumatra and in the Malay peninsula. Since Andersen wrote the Malaysian range of *lagochilus* has been much extended, Chasen (1940) for example recording it from as far west as Peninsular Thailand, Malaya and Nias Island, off west Sumatra, while Lekagul & McNeely (1977) record specimens (as *M. minimus*) from southeastern Thailand and Vietnam. It has not, however, been recorded from Java.

The directionality of the nares and the extent and depth of the internarial groove are characters that are sometimes variable or subjective, distorted in preserved specimens and sometimes difficult to observe. Goodwin (1979) for example was unable to discern any difference in the direction in which the nostrils face between Malayan *sobrinus* and *lagochilus* from Malaya, Sulawesi and the Solomon Islands, although this author pointed out that in *lagochilus* the margins of the nares are raised to show a tendency towards the development of incipient tubes.

Specimens in the British Museum (Natural History) establish quite clearly the presence of two forms in Java. The larger of these (length of forearm (4) 45·5–48·1, condylobasal length (4) 26·4–26·9) has a long rostrum (length orbit–nares (5) 10·4–11·0) and the lower jaw projects forward beneath the incisors to form a distinct sub-square chin. The nostrils are not raised marginally to form an incipient tubular structure and the internarial groove is represented at most by a narrow linear depression extending about halfway to the upper lip, or is obsolete. These correspond to the form called *sobrinus* by Andersen (1911, 1912). The smaller (length of forearm (19) 39·5–44·2, condylobasal length (9) 22·8–25·3) has a short rostrum (length orbit–nares (10) 8·1–9·2) and the mandible slopes posteriorly beneath the incisors, with rarely any suggestion of a squarish chin. The nostrils show no suggestion of a tubular form, but the internarial groove extends as a narrow linear depression to the upper lip, which is not divided. These correspond to the form called *minimus* Geoffroy, 1810*a* by Andersen (loc. cit.). It is not certain to which of the two Javan forms Geoffroy's name refers and the syntypes apparently are lost (Andersen, 1912) but for the present it seems both convenient and sensible to retain Andersen's fixation of this appropriate name on to the smaller form. Similar smaller specimens come from Madura and Kangean Islands. Tate (1942*c*) clearly appreciated the differences between *minimus* and *sobrinus,* recording the former from Cheribon, Java and from Bali, and the latter from North Pagi Island, Mentawei Islands, off west Sumatra. Although direct sympatry has not been demonstrated the conclusion that these represent distinct species seems unavoidable.

The collections also contain specimens of the larger form from Sumatra, Nias Island, Simalur Island, Malaya, Thailand and the island of Koh Samui. These agree in every essential point with the limited Javan representation: following Andersen (1912) they should be referred to *sobrinus* which is considered to be a distinct species, ranging certainly from Burma and Thailand south through the Malay Peninsula and Sumatra to Java. Length of forearm (16) 44·2–49·8, condylobasal length (6) 25·4–28·6, and length orbit–nares (6) 10·1–11·7.

Medway (1978) differentiated the two forms in Malaya by the features of the head and rhinarium: in the smaller (hitherto called *lagochilus,* cf. Chasen, 1940) the head is shorter, the nostrils forward pointing, with a distinct median internarial groove extending to the upper lip and flanked by two smaller grooves while in the larger (*sobrinus*) he noted that the head is longer, the nostrils more upwardly directed, and the median groove vestigial. He called the smaller form *M. minimus minimus,* thereby implying the synonymy of *lagochilus* with the Javan *minimus.* However, specimens from Malaya, Borneo, the Philippine Islands and Sulawesi have the margins of the nares raised to form a slightly tubular structure as was noted by Goodwin (1979) of specimens from Timor, and they have generally a more prominent internarial groove than do specimens from Java. In these respects and in size they agree with *lagochilus* from the Molucca Islands and for this reason I maintain *lagochilus* as a distinct subspecies, extending from southern Thailand and southern Vietnam through the Malay Peninsula to Borneo, the Philippines, Sulawesi, the Molucca Islands and Timor. Apparently neither *M. minimus minimus* nor *M. minimus lagochilus* have been recorded from Sumatra but Chasen (1940) reported the latter (with *sobrinus*) from the island of Nias, off the west coast.

The species and subspecies of *Macroglossus* may be briefly summarised:

Macroglossus minimus (Geoffroy, 1810*a*)	
M. m. lagochilus Matschie, 1899	S. Thailand, S Vietnam, Malaya, Nias I, Sirhassen I, (?) Sri Buat I; (?) Bunguran I,

	North Natuna Is; Borneo to Philippine Is, Sulawesi, Peleng I, Sanghir Is and Molucca Is.
M. m. minimus (Geoffroy, 1810*a*)	Java, Bali, Madura I, Kangean Is.
M. m. nanus Matschie, 1899	Aru Is, Kei Is, Mysol I, New Guinea, Bismarck Archipelago, Admiralty Is; Queensland, Australia.
M. m. pygmaeus Andersen, 1911	Murray I, Torres Straits
M. m. microtus Andersen, 1911	Bougainville, San Christobal, Guadalcanal and Florida Is, Solomon Is.

McKean (1972) considered *M. m. pygmaeus* and *M. m. microtis* to be synonyms of *M. m. nanus.* His measurements, which do not include any of topotypes either of *pygmaeus* or of *microtis,* certainly suggest that this may be so.

Macroglossus sobrinus Andersen, 1911	
M. s. sobrinus Andersen, 1911	Burma and Thailand to Sumatra, Nias I, Krakatoa I and Java.
M. s. fraternus Chasen & Kloss, 1927	Sipora and Siberut Is, Mentawei Is.

Macroglossus minimus nanus Matschie, 1899

Macroglossus nanus Matschie, 1899 : 98. Lamellana, New Britain, Bismarck Archipelago.

SPECIMENS EXAMINED. Papua New Guinea: ♀ BM(NH) 73.1974 Victoria Bay, Kairiru ridge, NW end of Kairiru I, near Wewak, East Sepik (in alcohol; coll. Aberdeen University Exploration Society Expedition to New Guinea, 1973); ♀♀BM(NH) 75.1840 Sepik, BM(NH) 75.1841 Rauit, West Sepik, 3° 36′ S, 142° 15′ E (both in alcohol; coll. A. M. Jones, Aberdeen University Exploration Society); (?) ♀♀ BM(NH) 78.858–859 Sapi Creek Forest Reserve, near Baku, Gogol Valley, c. 40 m (in alcohol; coll. P. A. Morris); ♀ BM(NH) 80.530 Kuni, Morobe, 7° 22′ S, 147° 11′ E; 3 ♂♂ (1 yg.), 4 ♀♀ (1 yg.) BM(NH) 80.531–537 Buso, Morobe, 7° 17′ S, 147° 08′ E (all in alcohol; coll. B. H. Gaskell, 'Operation Drake').

New Britain, Bismarck Archipelago: ♀ ♂ BM(NH) 69.309–310 Kareeba Plantation, Keravat. 4° 18′ S, 152° 01′ E (skins, skulls; coll. J. I. Menzies).

REMARKS. Apart from the cranial and dental characters to which Andersen (1912) drew attention, *M. m. nanus* is generally a little smaller than *M. m. lagochilus,* the length of the forearm in *nanus* (13) 36·2–42·8, in *lagochilus* (32) 38·0–44·0. Specimens from the Aru Islands and the Bismarck Archipelago are similar to those from New Guinea with length of forearm (6) 36·3–38·7. Hitherto unrecorded examples in London include BM(NH) 37.2.16.1 from north of Eilanden R, West Irian, and BM(NH) 29.5.27.7 from Wasjor, also in West Irian. A single specimen, BM(NH) 15.3.5.5 from Piara, Cape York, Queensland, Australia agrees closely with *nanus* in size and length of rostrum rather than with *M. m. pygmaeus* from Murray Island, Torres Straits. Tate (1952) also recorded *M. m. nanus* from Cape York: McKean (1972) reports specimens from Australia.

Macroglossus sobrinus sobrinus Andersen, 1911

Macroglossus sobrinus Andersen, 1911 : 642. Gunong Igari, Perak, Malaya.

Specimens examined. Krakatoa I, 06° 10′ S, 105° 26′ E: ♀ BM(NH) 74.241 (in alcohol; coll. G. Lincoln).

Remarks. There appears to be no previous record of *Macroglossus* from Krakatoa: among bats, Dammerman (1938) reported only *Rousettus amplexicaudatus, Cynopterus brachyotis angulatus* (=*C. sphinx angulatus*), *Cynopterus horsfieldi minor* (=*C. h. lyoni*) and *Hipposideros diadema* from the island. This specimen has slightly forwardly directed nostrils and a moderate internarial groove that extends towards the upper lip as a narrow linear depression, but does not reach it. The keel beneath the mandibular symphysis is prominently developed into an anteriorly projecting, square chin. Length of forearm 45·7.

Macroglossus sobrinus fraternus Chasen & Kloss, 1927

Macroglossus minimus fraternus Chasen & Kloss 1927: 836, Sipora I. Mentawei Is, off west coast Sumatra.

Specimens examined. Siberut I, Mentawei Is, off west coast Sumatra: ♀, 4♂♂ BM(NH) 78.2921–2925 Base of Tetei Bulak, Sabeuleleu, Paitan R, off Saibi R (in alcohol; coll. J. J. Whitten).

Remarks. Chasen & Kloss (1927) referred an adult male from Siberut to *fraternus.* These specimens with length of forearm 49·3–50·9 agree in size with the original material examined by these authors, differing from the nominate subspecies in their greater dimensions. In all the nostrils open laterally and face to the side, and the internarial groove is obsolete or at best is represented by a shallow linear depression that does not extend anteriorly beyond the immediate internarial area. Possibly specimens reported by Tate (1942*c*) from North Pagi Island, Mentawei Islands as *M. minimus sobrinus* (=*M. sobrinus sobrinus*), of which he notes some are very large, also represent *M. s. fraternus*

Syconycteris australis papuana (Matschie, 1899)

Macroglossus (Syconycteris) papuanus Matschie, 1899: 95, 99. Andai, NW West Irian.

Specimens examined. Papua New Guinea: ♂, ♀ BM(NH) 69.311–312 Schrader Mts., above Kaironk, 8500 ft c. 5° 10′ S, 144° 26′ E; ♀♀ BM(NH) 69.313–314 Efogi, Owen Stanley Mts., c. 40 miles E of Port Moresby, 3000 ft, 9° 07′ S, 147° 42′ E (all skins, skulls; coll. J. I. Menzies); 6 ♂♂, 4 ♀♀ BM(NH) 73.1975–1984 Biip, ½ mile SE of Rauit, West Sepik, c. 1650 ft, 3° 36′ S, 142° 15′ E: 4♂♂ BM(NH) 73.1985–1988 Rauit, 1750 ft, 3° 36′ S, 142° 15′ E: 13 ♂♂, 8 ♀♀ (1 yg.) BM(NH) 73.1989–2009 Kairiru ridge, centre of Kairiru I, near Wewak, East Sepik, c. 2000 ft; 3♂♂, ♀ BM(NH) 73.2010–2013 Victoria Bay, NW end of Kairiru I: ♂ BM(NH) 73.2014 Sabor, E end of Kairiru I (all in alcohol); BM(NH) 74.339–374 Near Rauit, 3° 36′ S, 142° 15′ E (skulls only) (all coll. Aberdeen University Exploration Society Expedition to New Guinea, 1973); ♂ BM(NH) 75.1848 Wageo I. Schouten Is. East Sepik; 3 ♂♂ BM(NH) 75.1849–1851 St. Xaviers, Kairiru I, East Sepik, c. 3° 21′ S, 143° 36′ E; 4 ♂♂, 4 ♀♀ BM(NH) 75.1852–1859 Sepik (all in alcohol; coll. A. M. Jones, Aberdeen University Exploration Society); 3 ♂♂, 2 ♀♀ BM(NH) 76.381–385 Okapa, Eastern Highlands, 6500 ft (in alcohol, coll. H. King); ♀ BM(NH) 78.860 Baku, Gogol Valley, Madang (skin only); ♀♀ BM(NH) 78.861–862 Baiyer R, c. 50 km NW of Mt. Hagen, Western Highlands, 1300 m; ♀ BM(NH) 78.863 Sapi Creek Forest Reserve, near Baku, Gogol Valley, Madang, c. 40 m; ♀♀ BM(NH) 78.864–865 Baiyer R area, Western Highlands, c. 1300 m; ♂ BM(NH) Mt. Hagen (town), Western Highlands (all in alcohol) (all coll. P. A. Morris); ♂ BM(NH) 80.538 7 km WSW of Buso, Morobe; ♂ BM(NH) 80.539 Rasange, Morobe; ♀ BM(NH) 80.540 Mt. Misson, Wau, Morobe; 15 ♂♂, 7 ♀♀, 2 (?) BM(NH) 80.541–564 Buso, Morobe (all in alcohol; coll. B. H. Gaskell, 'Operation Drake').

Discussion. Andersen (1912) recognised three species of *Syconycteris*, separated only by the features of the post-canine dentition, the last premolars (pm$\frac{4}{4}$) and first molar (m$\frac{1}{1}$) in *S. crassa* (Thomas, 1895) being elongate and decidedly more than half as wide as long, those of *S. australis* (Peters, 1867*a*) linear, their width only half their length, while *S. naias*

Andersen, 1911 was distinguished from the latter by the absence of the last upper (m^2) and lower (m$_3$) molars. At the time that Andersen wrote none had been found to be sympatric, *S. crassa* extending from Amboina in the Molucca Islands to New Guinea and some associated islands, *S. australis* occurring only in Queensland, and *S. naias* only on Woodlark Island in the Trobriand Islands. Tate (1942*c*) reported both *S. crassa* and *S. australis* from New Guinea, the two being collected together in the Central Division of Papua behind Port Moresby: Laurie & Hill (1954) followed the arrangement proposed by Andersen and implicitly adopted by Tate. Since then a highland species, *S. hobbit* Ziegler, 1982 has been described.

Lidicker and Ziegler (1968) reported a high degree of variability in the number of post-canine teeth in specimens of the *australis* type from the islands off southeastern New Guinea, including Woodlark, with the post-canine formula varying from $\frac{4}{5}$ to $\frac{5}{6}$ and exceptionally to $\frac{5}{7}$, as a result considering *naias* to be no more than subspecifically distinct from *australis.* A similar incidence of dental anomalies, the absence of one to four molars, or the presence of one or two supernumerary molars, was found by McKean (1972) in a large number of specimens referred to *australis* or to *crassa.* This author considered *naias* and *australis* synonymous, and pointed out that Brass (1959) had already recorded the latter, apparently with normal dentition, from Woodlark Island. Moreover, McKean found that in a large series of specimens from Papua New Guinea that he referred to *crassa* some had teeth nearly as narrow as *australis,* while a few juveniles without fully developed teeth could easily have been mistaken for that form. He concluded that but for the account by Tate (1942*c*) he would have considered *crassa* and *australis* only subspecifically related.

When first examined at the British Museum (Natural History) in 1974 the series of skulls (BM(NH) 74.339–374) led Hill (in Grieg-Smith, 1975) to the conclusion that *crassa* as understood by Andersen (1912) and Tate (1942*c*) could not be separated from *australis* since the dimensions of the relevant cheekteeth extended over most of the range of both alleged species. This variation does not conform to the definitions of Andersen or of Lidicker & Ziegler who redefined Andersen's dental criteria, pm$^4_4$ and m$^1_1$ according to these authors being less than one and one half times as long as broad in *crassa,* but in *australis* being one and one half times as long as broad, or more. Within the series now available pm^4 varies in length from approximately 110–200% of its width, pm$_4$ from 140–230%, m^1 from 100–180% and m$_1$ from 150–200%. Moreover, on occasion in a single specimen pm^4 and sometimes m^1 conform to the broader, elongate outline considered characteristic of *crassa* while pm$_4$ and m$_1$ are narrower and more linear, their proportions more nearly those ascribed to *australis.* The variation in tooth proportions is such that there is no point at which a division into two species on the basis of this character can be made.

Lidicker & Zeigler (1968) add that in *crassa* m^2 and m$_3$ are normally present although sometimes absent in *australis,* that the inner upper incisors tend to be slightly separated in *crassa* but in contact in its congener, and that the latter has shorter fur. McKean (vide supra) has demonstrated a wide degree of variation in the number of post-canine teeth in specimens from eastern New Guinea and this topic is also discussed in some detail by Koopman (1982) who concludes that molar number is not a good species character: among BM(NH) 74.339–374 only one specimen (74.344) has an obviously anomalous dental formula, lacking m^2 and m$_3$ on both sides. In this specimen, pm^4 and m^1 are sub-circular, pm$_4$ and m$_1$ rather more linear in outline, thus in the upper jaw conforming to the definition of *crassa,* in the mandible tending towards *australis.*

The series includes specimens which have the inner upper incisors convergent, in contact, very slightly separated, or not at all convergent and more distantly separated by a narrow but obvious interspace. However, this variation does not correlate with the features of pm$^4_4$ and m$^1_1$. At the extremes, BM(NH) 74.339 for example has inner upper incisors that stand separately but has strongly linear pm$^4_4$ and m$^1_1$, while BM(NH) 74.343 has convergent incisors that touch but sub-circular pm^4 and m^1, their mandibular counterparts only slightly elongate and not at all linear. Koopman (1979) could find no dichotomy into broad and narrow toothed forms, while Ziegler (1982) in describing the montane species *S. hobbit* examined six of the specimens referred to *australis* or to *crassa* by Tate (1942*c*) and was unable to find any consistent differences in tooth dimensions that would differentiate the two putative species. Moreover, Ziegler also could not establish any external, cranial or dental characters to suggest such a distinction among the extensive representation of relevant *Syconycteris* in the Bernice P. Bishop Museum, Hawaii.

The recognition that *australis* is conspecific with *crassa* means that as the prior name *australis* must become the specific epithet and possibly the subspecific name for the population in New Guinea usually called *papuana.* However, Koopman (1979) remarked that Australian specimens of which he had seen a limited sample tend to be smaller than those from New Guinea and tentatively retains *australis* and *papuana* as distinct subspecies. The remaining subspecies of *S. australis* also seem only slightly differentiated. They include *crassa* (Thomas, 1895) from the islands southeast of New Guinea, *keyensis* Andersen, 1911 from the Kei Islands, *major* Andersen, 1911 from Amboina and Ceram Islands, in the Molucca Islands, and *finschi* (Matschie, 1899) from the Bismarck Archipelago. McKean (1972) synonymised *keyensis* and *finschi* with *papuana,* and regarded *naias* as a synonym of *australis* (=*S. australis australis*), Lidicker & Ziegler (vide supra) having considered the latter two to be subspecifically related as does Koopman (1982), who carried out a detailed examination of specimens from eastern Papua and its associated islands. However, Koopman (1979) retained *finschi* on account of its slightly smaller size when compared with *papuana*: measurements of BM(NH) 74.339–374 (condylobasal length 23·2–24·8, width of braincase 10·2–11·4) agree with those of New Guinea specimens measured by this author and support his contention. Possibly *naias* from Woodlark Island is synonymous with *australis* but may prove to be another weakly separable subspecies.

According to Zeigler (1982) the dorsal pelage of *S. australis* in any area is apparently slightly less dense and less woolly, inter alia, than that of *S. hobbit,* the two so far being found to be sympatric only at Mount Kaindi, Morobe, Papua New Guinea. The two specimens (BM(NH) 69.311–312) of *S. australis* reported here from the Schrader Mountains at 8500 ft have longer, slightly denser fur than do those from lower locations, and are also a little darker in overall coloration, thus confirming the observation by Ziegler that high level examples were the darkest to be found in the species. It seems possible that a high altitude subspecies of *S. australis,* which according to Ziegler occurs as high as at least 3000 m, might be recognised in due course.

Syconycteris australis major Andersen 1911

Syconycteris crassa major Andersen, 1911 : 643, Amboina I. Molucca Is.

SPECIMENS EXAMINED. Molucca Is: ♂♂ BM(NH) 81.1126–1127 Kaiteto, Amboina I (in alcohol; coll. B. H. Gaskell, 'Operation Drake').

REMARKS. In length of forearm (46·0, 47·5) these specimens fall within the range given by Andersen (1911, 1912) for this larger subspecies.

Notopteris macdonaldi macdonaldi Gray, 1859

Notopteris macdonaldi Gray, 1859 : 38, pl. 67. Viti Levu I, Fiji Is.

SPECIMENS EXAMINED. Fiji Is: 6 ♂♂, 6 ♀♀ (1 yg.) BM(NH) 78.2394–2405 Saweni Navosi/Koro Bulia, Sigatoka Valley, Viti Levu I, 17° 39′ S, 177° 30′ E (skins, skulls; coll. J. C. Pernetta).

New Hebrides: ♂♂ BM(NH) 73.1319–1320 (1 yg.) Analghaut Village, Aneityum I, near sea level; 3 ♂♂, ♀ BM(NH) 73.1321–1324 About 2 km E of 'Bethel', Tanna I, 120 m; 3 ♂♂ (2 nurselings), 4 ♀♀, 1 (?) BM(NH) 73.1325–1332 Watantup, about 4 miles N of Ipota, east coast Erromanga I, at sea level; ♂ BM(NH) 73.1333 Nokowoula, Espiritu Santo I, 3700 ft (all in alcohol except BM(NH) 73.1331–1332, skins; coll. or obtained by the Earl of Cranbrook, Royal Society Expedition to the New Hebrides, 1971).

REMARKS. Specimens obtained by the Royal Society Expedition in 1971 extend *N. macdonaldi* to most of the major islands of the New Hebrides, whence before it has been known in the literature apparently only from Aneityum (Andersen, 1912). The collections of the British Museum (Natural History) also include two females (BM(NH) 26.6.4.7–8) from Efate Island.

DISCUSSION. The two subspecies of *N. macdonaldi*, *N. m. macdonaldi* (Fiji Is and New Hebrides) and *N. m. neocaledonica* Trouessart, 1908 (New Caledonia) differ chiefly in the smaller size of the latter (Andersen, 1912, Revilliod, 1914, Sanborn & Nicholson, 1950): specimens in the collections of the British Museum (Natural History) suggest also that generally *neocaledonica* has a lower, rather less massive rostrum than *macdonaldi*. Measurements given by Revilliod (1914) and by Sanborn & Nicholson (1950) when comparing Fijian *macdonaldi* with *neocaldonica* indicate a considerable difference in forearm length that is not entirely supported by specimens in London. Sanborn & Nicholson in fact suggested that the forearm length of Fijian *macdonaldi* is always longer than in *neocaledonica*, although they had seen no adult male of this latter subspecies. These authors indicated that in Fijian *macdonaldi* the length of the forearm did not fall below 63·9 and that in *neocaledonica* it did not exceed 61·5. However, a series of specimens (BM(NH) 19.10.8.5–15) from Mount Tambignon, New Caledonia, at 2500 ft have forearms ranging in length from 60·2–63·4 in males and in females from 60·3–64·3.

Specimens from the Fiji Islands and from the New Hebrides tend to further bridge the alleged size difference. Six Fijian males range in forearm length from 63·5–68·8 (but Sanborn & Nicholson (1950) report a male of 71·3), five females from 63·0–66·0. In the New Hebrides a male from Aneityum has a forearm length of 69·9 and a female (BM(NH) 25.12.14.11) of 65·1. Three males from Tanna have forearms varying in length from 65·0–69·0, a female a forearm length of 62·8. The adult male from Erromanga has a forearm length of 61·5, four females from the same island having forearms ranging in length from 61·6–63·6, while the adult but not old male from Espiritu Santo has a forearm length of 64·8.

Sanborn & Nicholson (1950) reported the presence of a strong sagittal crest extending from the frontals to well-developed lambdoidal crests in males of *N. m. macdonaldi*, females lacking a sagittal crest but possessing similar well-developed lambdoidal crests. A slightly less developed sagittal crest is also present in the older males of *N. m. neocaledonica*.

MICROCHIROPTERA

EMBALLONURIDAE

Emballonura alecto alecto (Eydoux & Gervais, 1836)

Vespertilio (Nycticeius) alecto Eydoux & Gervais, 1836 : 7. Manila, Luzon I, Philippine Is.

SPECIMENS EXAMINED. C Sulawesi: ♂♂ BM(NH) 82.1–16 Tapu Waru, 1° 55′ S, 121° 22′ E; ♀ BM(NH) 82.17 Ganda Ganda, 1° 57′ S, 121° 21′ E; ♀, ♂ BM(NH) 82.18–19 Tarongga, 1° 44′ S, 121° 40′ E (all in alcohol, skulls of BM(NH) 82.1–5, 82.13 extracted; coll. B. H. Gaskell, 'Operation Drake').

REMARKS. These specimens are referred to *E. alecto* rather than to the closely similar species *E. monticola* Temminck, 1838 by virtue of their rather large skulls which have a relatively long antemolar region, with a marked diastema between the first upper premolar (pm^2) and the second upper premolar (pm^4). Tate & Archbold (1939) recorded *E. alecto* from Likeopang, north Sulawesi and from Peleng Island on the basis of specimens in the United States National Museum of Natural History, Washington. These are evidently those reported among others (in this case from Limpoeang) by Shamel (1940) as *E. monticola rivalis* Thomas, 1915*c* (=*E. alecto rivalis*). Although comparative material is limited, specimens from Sulawesi and the Molucca Islands agree most closely in several points of size with examples from the Philippine islands and are referred to the nominate subspecies.

Emballonura monticola also occurs in Sulawesi whence it has been recorded from the southern part of the island by Tate & Archbold (1939).

Measurements of specimens from Sulawesi: length of forearm (19) 43·1–48·3; greatest length of skull (6) 14·7–15·1; condylobasal length (6) 13·5–14·0; condylocanine length (6) 12·9–13·2; width of rostral swellings (6) 5·9–6·2; least interorbital width (4) 4·7–5·0; least postorbital width (6) 2·7–3·0; zygomatic width (5) 8·7–9·1; width of braincase (6) 6·8–7·1; mastoid width (6) 7·5–8·2; c^1–c^1 (alveoli) (6) 3·6–4·0; m^3–m^3 (6) 6·1–6·4; c–m^3 (6) 5·5–5·7; length complete mandible from condyles (4) 9·8–10·0; length right ramus from condyle (6) 10·1–10·6; c–m_3 (6) 5·6–5·9.

Emballonura nigrescens papuanus Thomas, 1914

Emballonura papuanus Thomas, 1914*b* : 443. Wakatimi, Mimika R, SW west Irian.

Specimens examined. Papua New Guinea: ♂ BM(NH) 80.606 Buso, Morobe, 7° 17′ S, 147° 08′ E (in alcohol; coll. B. H. Gaskell, 'Operation Drake').

C Sulawesi: ♂ BM(NH) 82.20 R Ranu, 1° 51′ S, 121° 30′ E (in alcohol, skull extracted; coll. B. H. Gaskell, 'Operation Drake').

Remarks. The short, blunt muzzle, widely separated elliptical nostrils and long, narrow tragus with backwardly directed tip quite clearly refer these specimens to *E. nigrescens.* The example from Sulawesi has a slightly larger and more inflated braincase than *E. n. nigrescens* (Gray, 1843*a* from the Moluccan islands of Amboina, Buru and Ceram and on this account is referred to *E. n. papuanus,* otherwise known from Ternate Island, New Guinea and the Schouten and Kei Islands. According to Thomas (1914*b*) the rostrum of *E. n. papuanus,* is also short and stumpy but this feature is not at all obvious in the series in the British Museum (Natural History). Tate & Archbold (1939) and Shamel (1940) have also recorded the subspecies from Sulawesi. Measurements of the Sulawesian example BM(NH) 82.20: length of forearm 32·2; greatest length of skull 11·0; condylobasal length 10·4; condylocanine length 10·2; width rostral swellings 4·0; least interorbital width 3·0; least postorbital width 2·3; zygomatic width —; width of braincase 6·0; mastoid width 6·2; c^1–c^1 (alveoli) 3·0; m^3–m^3 5·1; c–m^3 4·2; length complete mandible from condyles —; length right ramus from condyle 7·9; c–m_3 4·4.

Taphozous melanopogon Temminck, 1841

Taphozous melanopogon Temminck, 1841 : 287, pl. 60, figs. 8, 9. Bantam, W Java.

Specimens examined. S. Sulawesi: ♀♀ BM(NH) 82.12–22 Lalonggasu Meeto, (Tomba Watu Cave), 18 km from Kendari Central (in alcohol, skulls (of BM(NH) 81.22 fragmentary) extracted; coll. B. H. Gaskell, 'Operation Drake').

Remarks. Although these specimens have relatively long forearms, the distribution of the fur at the sides of the body, unlengthened rostrum, rather narrow, elongate braincase and smaller teeth, especially the canines, suggests that they should be referred to *T. melanopogon* rather than to the closely similar species *T. theobaldi* Dobson, 1872*a.* The latter was reported from Java by Thomas & Wroughton (1909) on the basis of specimens now in the collections of the British Museum (Natural History): these, although smaller than a very limited sample of *T. theobaldi* from India, Burma and Thailand have longer forearms (71·1–72·5 in ten examples) than the specimens from Sulawesi here referred to *T. melanopogon,* and their skulls are generally larger. Unfortunately, few specimens of *T. melanopogon* are known from Java: the species occurs otherwise from India and southern China to the Philippine Islands and the islands of Sumbawa, Savu and Timor in the Lesser

Sunda chain. These from Sulawesi are the first of *T. melanopogon* to be recorded from that island: in size they are similar to those reported by Goodwin (1979) from Timor, or to *T. m. achates* Thomas, 1915*b* from Savu Island.

Measurements (BM(NH) 82.21, 82.22): length of forearm 68·5, 67·7; greatest length of skull —, —; condylobasal length —, —; condylocanine length 21·6, —; least interorbital width 6·4, 6·4; least postorbital width 5·3; —; zygomatic width 13·1, —; width of braincase 10·3, —; mastoid width 11·6, —; c^1–c^1 (alveoli) 4·3, —; m^3–m^3 9·3; —; c–m^3 9·8, 9·5; length complete mandible from condyles 16·8, 16·4; length right ramus from condyle 17·4, 16·9; c–m_3 10·7, 10·4.

Discussion. The genus *Taphozous* has remained unrecorded from Sulawesi until comparatively recently, although its overall Oriental distribution from the Indian subcontinent to the Philippine Islands and Australia clearly indicates that it might be expected to occur on that island. Apart from *T. (Taphozous) melanopogon,* the pouch-bearing bat *T. (Saccolaimus) saccolaimus* Temminck, 1841 has been reported lately from Sulawesi, Fieler (1980) having identified an old specimen dating from 1883 in the Staatliches Museum für Tierkunde, Dresden as an example of this species. It has been known to occur hitherto from India to Borneo, Java and Timor, and may extend to New Guinea, the Solomon Islands, the Northern Territory of Australia and northeastern Queensland if *nudicluniatus* De Vis, 1905 is conspecific with *saccolaimus* as Goodwin (1979), McKean *et al.* (1980) and Koopman (1982) suggest.

MEGADERMATIDAE

Megadema spasma niasense Lyon, 1916

Megaderma niasense Lyon, 1916 : 440. Nias I, off W Sumatra.

Specimens examined. Siberut I, Mentawei Is: ♂♂ BM(NH) 78.2926–2928 Near Sibosua R, Paitan R, off Saibi R; ♀♀ BM(NH) 78.2929–2931 Ridge to the E of Sibosua R (all in alcohol, skulls of BM(NH) 78.2929–2930 extracted; coll. J. J. Whitten).

Remarks. There is no previously published record of *M. spasma* from Siberut although the species has been recorded widely (Lyon, 1916, Chasen, 1940) from the island chain of which Siberut forms a part. These specimens agree in many respects with the description of *naisense* from the island of Nias to the northwest of Siberut: they are a little smaller on the whole than *M. s. trifolium* Geoffroy, 1810*b* from Java and southern Sumatra, with the parts of the maxillae over the canines less enlarged and the tympanic bullae and teeth generally smaller. External measurements: length of forearm (6) 55·9–58·8; length of ear (6) 32·0–33·4; length of tibia (6) 31·1–32·2. Cranial measurements (BM(NH) 78.2929, 78.2930): greatest length of skull 24·8, 25·5; condylocanine length 21·5, 22·8; least interorbital width 3·9, 4·0; zygomatic width 13·6, 14·1; width of braincase 10·5, 10·3; mastoid width 11·0, 11·5; c^1–c^1 (alveoli) 4·8, 5·1; m^3–m^3 8·0, 8·3; c–m^3 9·2, 9·9; length complete mandible from condyles 16·1, 17·3; length right ramus from condyle 16·7, 17·9; c–m_3 10·1, 10·9.

Megaderma spasma celebensis Shamel, 1940

Megaderma spasma celebensis Shamel, 1940 : 352. Likoepang, Sulawesi.

Specimens examined. C Sulawesi: 3♀♀, 2 ♂♂ BM(NH) 82.23–27 Ganda Ganda, 1° 57′ S, 121° 21′ E; 5 ♂♂, 3 ♀♀ Songinbau, 1° 46′ S, 121° 43′ E (all in alcohol, skulls of BM(NH) 82.24–27, 82.29–31, 82.33, 82.35 extracted; coll. B. H. Gaskell, 'Operation Drake').

Remarks. Andersen & Wroughton (1910) and Andersen (1918) referred specimens of *M. spasma* (Linnaeus, 1758) from Sulawesi and from the Philippine Islands to the nominate subspecies, also known from its type locality, Ternate Island in the northern Moluccas. Later, Shamel (1940) separated Sulawesian material as *M. s. celebensis* on account of its generally smaller skull and the absence of any distinct contrast in colour between the dorsal and ventral surfaces of the body. Tate (1941*b*) who evidently had not seen the account by Shamel considered specimens from Sulawesi inseparable from those from Java, presumably *M. s. trifolium.*

This series of Sulawesian specimens from 'Operation Drake' confirms the small cranial size noted by Shamel (1940) when describing *celebensis*: all agree in size with those from Sulawesi measured by this author and are rather smaller than the Philippine specimens that he examined. They are also somewhat smaller than a series of *M. s. trifolium* from Java.

Measurements: length of forearm (13) 52·2–57·1; length of ear (13) 35·3–37·4; length of tibia (13) 29·2–30·5; greatest length of skull (9) 23·9–24·4; condylocanine length (9) 21·1–21·6; least interorbital width (9) 3·7–4·0; zygomatic width (9) 13·3–14·0; width of braincase (9) 9·9–10·7; mastoid width (8) 10·5–11·0; c^1–c^1 (alveoli) (9) 4·6–5·0; m^3–m^3 (9) 7·4–8·1; c–m^3 (9) 8·8–9·3; length complete mandible from condyles (9) 15·4–16·1; length right ramus from condyle (9) 16·2–16·6; c–m_3 (9) 9·9–10·3. Fourteen examples of *M. s. trifolium* from Java have a condylocanine length of 21·8–23·4 and a length c–m^3 of 9·3–9·8: three from Kangean Island are of similar size with corresponding measurements of 21·8–22·5 and 9·2–9·5.

RHINOLOPHIDAE

Rhinolophus celebensis celebensis Andersen, 1905

Rhinolophus celebensis Andersen, 1905*a* : 83, pl. 3, figs. 4a, 4b, Makassar, S Sulawesi

Specimens examined. C Sulawesi: ♀ BM(NH) 82.36 R Ranu, 1° 51′ S, 121° 30′ E; 5 ♂♂, 5 ♀♀ BM(NH) 82.37–46 Songinbau, 1° 46′ S, 121° 43′ E; ♀♀ BM(NH) 82.47–48 Taronggo, 1° 44′ S, 121° 40′ E: ♂, ♀ BM(NH) 82.49–50 Kabalo, Mt. Tambusisi, c. 300 m, 1° 40′ S, 121° 20′ E (all in alcohol, skulls of BM(NH) 82.36–37, 82.39–40, 82.48, 82.50 extracted; coll. B. H. Gaskell, 'Operation Drake').

Remarks. These specimens agree favourably with the holotype of *R. c. celebensis* and with the limited sample of this taxon in the collections of the British Museum (Natural History). They supplement the records of *celebensis* from various localities in Sulawesi by Andersen (1905*a*), Tate & Archbold (1939) and Bergmans & Rozendaal (1982). Measurements: length of forearm (15) 39·7–43·4; condylocanine length (6) 15·5–16·0; supraorbital length (junction of supraorbital crests to nares) (6) 5·0–5·1; palatal length (6) 2·0–2·3; length rostral inflations (6) 1·9–2·1; width rostral inflations (6) 3·1–3·6; width of rostrum (6) 4·6–5·0; least interorbital width (6) 2·1–2·4; zygomatic width (6) 8·7–9·0; width of braincase (6) 7·4–7·7; mastoid width (6) 8·4–8·7; c^1–c^1 (alveoli) (6) 4·2–4·6; m^3–m^3 (6) 6·3–6·5; c–m_3 (6) 6·8–7·1; length complete mandible from condyles (5) 11·6–11·7; length right ramus from condyle (5) 11·9–12·0; c–m_3 (6) 6·8–7·1.

Discussion. Goodwin (1979) in describing *parvus* from the island of Timor discussed the relationships of *celebensis* to *borneensis* Peters, 1861 from Borneo and to *javanicus* Andersen, 1918 from Java, concluding that all belonged to the same species, *R. borneensis.* This author remarked that the most useful taxonomic features of the skull in the *borneensis* group (sic) are the size and shape of the anterior median nasal inflations, the width of the interorbital constriction, and the position of the junction of the supraorbital crests, characters also used for the most part by Andersen (1905*a*) in his classic study of the complex to which these forms belong, the *simplex* group of Andersen, 1905*a* or *megaphyllus* group of Andersen, 1918, later renamed the *ferrumequinum* group by Tate & Archbold, 1939. Apart from those already mentioned, named taxa immediately relevant to this question also include *importunus* Chasen, 1939 from eastern Java, *madurenesis* Andersen, 1918 from the nearby island of Madura, *spadix* Miller, 1901 from the South Natuna and Karimata Islands and *chaseni* Sanborn, 1939 from Con Son Island (Pulo Condore), off the southeastern coast of Indochina.

The small series of *celebensis* reported here confirms the general similarity to *borneensis* suggested by Andersen (1905*a*) and formalised by Goodwin (1979) in considering the two conspecific. There is some variability in the size and shape of the anterior median narial inflations: the holotype (BM(NH) 97.1.3.19) of *celebensis* has rather short inflations which in other examples are longer antero-posteriorly. On the whole the anterior narial inflations are a little smaller than those of a limited sample of *borneensis* but the smallest of *borneensis* are closely similar to the largest of *celebensis*. The narial inflations of *celebensis* are less inflated than those of *R. keyensis* Peters, 1871 from the Molucca Islands to the east, although generally similarly narrow, and in this species the facial part of the skull tends to be longer than in *celebensis*, with the junction of the supraorbital and the sagittal crests lying at a point more or less behind the middle of the orbit rather than more or less in front of it. As Goodwin (1979) pointed out, *borneensis* differs more from *celebensis* and its immediate allies *javanicus* and *parvus* than these do from each other in its more strongly arched fronto-parietal area and more bulbous occipital region, although these characters are less clear when series are examined. In addition to the generally larger and wider narial inflations and more inflated braincase, *borneensis* and its close allies *spadix* and *chaseni* are usually a little larger cranially than any of the more easterly forms. Goodwin (1979) omitted any mention of *madurensis* in his account of *parvus*, to which in fact it is similar in size and structure. Comparison suggests that details of coloration apart (the sole *parvus* available is in alcohol) the two may be separated only by the slightly less globular narial inflations of *madurensis*. It should be noted that the 'condylocanine length' given by Goodwin (1979 : 107, tab. 1) for *parvus, javanicus, celebensis* and *borneensis* is in fact the greatest length of the skull.

Through the courtesy of Dr C. J. Smeenk of the Rijksmuseum van Naturlijke Historie, Leiden it has been possible to examine one (RMNH 15320) of the original specimens of *importunus* Chasen, 1939 from Tjiawitali, near Wijnkoops Bay, east Java. Further comparison confirms the view expressed by Chasen in the original account that cranially it is very like *borneensis*, with which it agrees in size, inflated braincase and bulbous occipital region, differing in these features from *javanicus*, known so far from west Java. As Chasen pointed out, it is clearly very closely related to *borneensis* to which it is very similar. Although admitting this close relationship and also indicating clearly that it could not be placed with *javanicus* he was reluctant to unite *importunus* with *borneensis* largely because the known occurrences of *importunus* in eastern Java and of *javanicus* in western Java might imply that they replaced each other geographically. However, further examination leaves little doubt that *importunus* must be allied with *borneensis*.

For these reasons and in view of the limited material as yet available for some of the forms involved, I prefer to retain *borneensis* and *celebensis* as distinct species, the latter to include *javanicus, madurensis* and *parvus* as subspecies, although the very small size of *madurensis* and *parvus* might justify their specific distinction (as *madurensis*) from *celebensis*. *Rhinolophus borneensis* includes *spadix, chaseni* and *importunus* as subspecies, the last possibly occurring sympatrically with *R. celebensis javanicus* in Java. Possibly the very small *virgo* Andersen, 1905*a* from Luzon Island, Philippine Islands should also be associated with *R. celebensis*, while *nereis* Andersen, 1905*a* from Pulo Siantan, Anamba Islands evidently represents *R. borneensis*, but is considerably larger.

Rhinolophus pusillus pusillus Temminck, 1834

Rhinolophus pusillus Temminck, 1834 : 28, pl. 1, fig. 9. Java.

SPECIMENS EXAMINED. Borneo: ♂ BM(NH) 78.2491 About 25 km inland from Sangkulirang, a small port at the mouth of the R Baa, East Kalimantan, c. 0° 59′ N, 117° 55′ E (in alcohol, skull extracted; coll. S. M. Jeffrey).

Remarks. Although known from India and southern China to the Anamba Islands, Java and Madura Island, *R. pusillus* has not been recorded hitherto from Borneo. In size this specimen agrees closely with those from Java and the smaller islands of Madura, Tioman and Penang recorded by Hill (1974) and also with the skin from Aur (=Aor) Island reported earlier by this author (1960) as of *R. minutillus* Miller, 1906*a* (=*R. pusillus minutillus*, originally described by Miller (1900) as *R. minutus*) from Siantan Island, Anamba Islands. Specimens from the Malayan offshore islands, Madura Island and Borneo all seem referrable to the nominate subspecies *R. p. pusillus.*

Measurements of BM(NH) 78.2491: length of forearm 37·0; greatest length of skull to canine 15·6; condylocanine length 13·8; width across rostral swellings 4·1; least interorbital width 2·1; zygomatic width —; width of braincase 7·0; mastoid width 7·9; c^1–c^1 (alveoli) 3·8; m^3–m^3 5·8; length complete mandible from condyles 9·9; length right ramus from condyle 10·3; c–m_3 6·2.

Rhinolopus euryotis tatar Bergmans & Rozendaal, 1982

Rhinolophus tatar Bergmans & Rozendaal, 1982 : 170. Moinakom River, Dumoga Nature Reserve, North Sulawesi, 525 m, 0° 41′ M. 124° 03′ E.

Specimens examined. C Sulawesi: 9 ♂♂, 17 ♀♀ BM(NH) 82.51–76 Songinbau, 1° 46′ N, 121° 43′ E; 12 ♂♂, 7 ♀♀ BM(NH) 82.77–95 Taronggo, 1° 44′ N, 121° 40′ E; ♀ BM(NH) 82.96 R Ranu, 1° 51′ S, 121° 30′ E (all in alcohol, skulls of BM(NH) 82.51, 82.53–55, 82.78–82, 92.84–88, 82.90 extracted; coll. B. H. Gaskell, 'Operation Drake').

S Sulawesi: ♂♂ BM(NH) 82.97–98 Lalonggasu Meeto (Tomba Watu Cave), 18 km from Kendari Central (in alcohol, skull of BM(NH) 82.98 extracted; coll. B. H. Gaskell, 'Operation Drake').

Remarks. This subspecies (length of forearm 48·4–53·2) includes the smallest of *R. euryotis,* with broad noseleaf that covers the muzzle, the anterior leaf with a very shallow emargination, the margins of this notch thickened, the thickening extending posteriorly as narrow ridges over the leaf to delimit a shallow longitudinal median groove terminating at the edge of the narial depression in a small, thickened, posteriorly directed projection. The internarial region is expanded laterally into a wide, angular cup and the sella is wide, slightly ovate-pyriform in frontal outline. Its connecting process is high, arcuate and inserted anteriorly at or near the upper margin of the sella, with a lower insertion posteriorly on the intermediate part of the leaf. The lancet is high, cuneate, with an acute point, and is densely pilose. The ears are large, extending to the tip of the muzzle when laid forward; their anterior or medial margin is convex beneath a small, acutely pointed tip, their posterior margin concave just beneath tip, otherwise convex with a well developed more or less rectangular antitragal lobe.

The skull is relatively small with short, broad rostrum and elongate braincase, the anterior median rostral inflations relatively large, swollen, projecting, high and rounded and there is a shallow triangular frontal depression bounded laterally by moderate suprorbital ridges. The median cranial crest is well developed, more evident anteriorly than posteriorly and the zygomata are not greatly expanded, the zygomatic width subequal to or only slightly exceeding the mastoid width. The palate is short, its length one third or less the length of the maxillary toothrow and the cochleae are expanded, only narrowly separated basioccipitally. The anterior upper premolar (pm^2) is small, in the toothrow, not compressed and the second lower premolar (pm_3) is very small, extruded from the row.

Externally this subspecies may be distinguished from the other described forms of *R. euryotis* by its shorter forearm, generally smaller size, and, for the most part, by its narrower sella which is usually less expanded laterally and often less ovate-pyriform than in the other members of the species. In the majority of its features it is most similar to *R. e. aruensis* Andersen, 1907*b* (Aru Islands) or to *R. e. burius* Hinton, 1925 (Buru Island, Molucca Islands) but has a less massive and narrower rostrum, slightly less inflated braincase and slightly smaller and less massive teeth, especially the canines. Its shorter forearm and narrower sella provide obvious features distinguishing *tatar* from *R. e. euryotis* Temminck, 1835 (Amboina and Ceram Islands, Molucca Islands), *R. e. timidus* Andersen, 1905*b* (Batchian Island and New Guinea) and from *R. e. praestans* Andersen, 1905*b* (Kei Islands): in these, especially in *R. e. euryotis,* the noseleaf is more fleshy and the features of the antenarial region more greatly developed, with a more emphatic longitudinal groove across the anterior leaf terminating in a larger posterior projection.

DISCUSSION. Tate & Archbold (1939) provided the first reports of *R. euryotis* from Sulawesi, recording specimens from the south and southeast of the island. These authors thought Sulawesian specimens most probably referable to *R. e. euryotis,* although apparently they had not examined specimens from Amboina, its type locality, or any of the other associated islands in the Moluccas. They relied instead on the description of *euryotis* by Temminck (1835) and in particular upon his statement that the forearm in Amboinese specimens measured '2 pouces' which they converted as 50·8 mm. They remarked that the treatment by Andersen (1905*b*) of *euryotis* was somewhat invalidated by the assumption that the forearm of the nominate subspecies was 56 mm in length, against this lower figure given by its describer, and postulated larger subspecies (*praestans, timidus* and *burius)* in the Kei Islands, Batchian and New Guinea, and on Buru, with smaller subspecies (*aruensis, euryotis*) in the Aru Islands and in Amboina and Sulawesi. Specimens reported by these authors from Sulawesi agree closely in size with *tatar* as described by Bergmans & Rozendaal (1982) and with the specimens reported here.

A small series of *R. euryotis* in the collections of the British Museum (Natural History) from Amboina and the nearby island of Ceram has forearm lengths ranging from 55·1–58·4, considerably larger than the value assumed by Tate & Archbold (1939) for Amboinese specimens. In fact, these authors have converted Temminck's measurements as English pouces (one pouce = 25·4 mm), but Temminck used the French equivalent (one pouce = 27·07 mm) which when converted gives a value of 54·1 mm, much closer to the forearm lengths of Amboinese specimens available in London. This deduction is confirmed by Bergmans & Rozendaal (1982) who quote approximate forearm lengths (measured by Dr C. J. Smeenk) of 54·9, 55·1 and 54·5 for the three syntypes of *euryotis* in the Rijksmuseum van Natuurlijke Historie, Leiden.

The specimens reported here agree exactly with the description of *tatar* by Bergmans & Rozendaal, who considered it a distinct species, morphologically nearest to *R. arcuatus* Peters, 1871. This latter species is widely distributed from Luzon Island (*arcuatus*) and Mindanao Island (*exiguus* Andersen, 1905*b*) in the Philippine Islands to Borneo (*proconsulis* Hill, 1959), Sumatra (*beccarii* Andersen, 1907*c*), Buru Island in the Molucca Islands (*toxopeusi* Hinton, 1925), Wetter Island in the Flores Sea (*angustifolius* Sanborn, 1939) (thought probably a distinct species by Bergmans & Rozendaal, 1982) and New Guinea (*mcintyrei* Hill & Schlitter, 1982). Although very similar both externally and cranially to *R. euryotis,* its anterior noseleaf lacks the characteristic broad median groove of this species flanked by swollen longitudinal ridges and extending across the leaf to the internarial region, where it terminates at a small projection. Instead, the narrow anterior emargination of the leaf is prolonged posteriorly as a narrow linear groove onto the face of the leaf, this groove extending less than halfway to the internarial region. Moreover, although the largest of *R. arcuatus* (*proconsulis, mcintyrei*) have forearm lengths that reach or overlap those *tatar* the skull is slightly smaller, with smaller teeth.

When first examined the specimens reported here were referred to *R. euryotis*: although they differ sharply from *R. e. euryotis* in size and in the lesser degree of development of the antenarial structures they are closely approached in the former respect by *R. e. aruensis* and in the latter by this subspecies and to some extent by *R. e. burius.* Specimens of *R. e. praestans* and *R. e. timidus* are nearer to *R. e. euryotis* in these features. As Bergmans & Rozendaal (1982) pointed out, in comparison with *R. euryotis* the teeth of *tatar* are not small, the zygomatic width is not narrowed and the sagittal crest is not low. Consequently, they considered the skull of *tatar* to display a tendency towards *R. euryotis* although on its

Table 4 Selected measurements of *Rhinolophus euryotis* (numbers of specimens examined in parentheses)

	R. e. tatar	*R. e. euryotis*	*R. e. burius*	*R. e. praestans*	*R. e. aruensis*	*R. e. timidus*	Kiriwina I (ex Koopman, 1982)	New Britain (ex Koopman, 1982)	New Britain (ex Smith & Hood, 1981)
Length of forearm	(48) 48·4–53·1	(11) 55·1–58·4	55·1	(8) 55·5–58·0	53·1, 54·1	(11) 53·9–57·3	(1) 52	51	57·4
Width of sella	(48) 2·8–3·6	3·7, 3·8	3·5	(5) 3·9–4·1	3·7, 3·9	(7) 3·9, 4·5			
Condylocanine length	(16) 19·5–21·0	(6) 20·9–22·5	21·0	(8) 21·4–22·4	20·8, 21·0	21·3, 22·5	(2) 20·1, 20·4	21·1	
Rostral width	(16) 5·8–6·5	(7) 6·5–7·4	6·7	(8) 6·6–7·1	6·6, 6·6	(3) 6·6–6·9			
Zygomatic width	(15) 10·7–11·3	(6) 11·7–12·6	12·2	(8) 12·0–12·6	11·5, 11·6	(3) 11·4–12·1			
Width of braincase	(16) 9·1–9·8	(6) 8·9–10·6	10·2	(8) 10·0–10·4	10·0, 10·2	(3) 9·9–10·1			
Mastoid width	(15) 10·4–11·2	(6) 11·0–11·7	11·1	(8) 11·1–11·6	11·0, 11·3	11·2, 11·4	(2) 10·7, 10·9	11·4	
m^3–m^3 (crowns)	(16) 8·1–8·4	(6) 8·7–9·3	9·0	(8) 9·1–9·5	8·8, 9·0	(3) 8·7–9·2	(3) 8·1–8·4	8·5	
m^3–m^3 (alveoli)	(16) 7·7–8·2	(7) 8·5–9·1	8·8	(8) 8·7–9·1	8·4, 8·5	(3) 8·4–8·6			
c–m^3	(16) 8·7–9·4	(7) 9·5–10·2	9·4	(8) 9·5–10·0	9·4, 9·6	(3) 9·4–9·8	(3) 8·8–9·2	9·5	

external features they considered *tatar* to be nearest to *R. arcuatus*. However, Bergmans & Rozendaal (1982) appear to have made no direct comparison with any representative of *R. arcuatus*, and of *R. euryotis* only with examples of the nominate subspecies from Amboina. Comparison with all but *angustifolius* among *R. arcuatus*, and with all of the described form of *R. euryotis* leads me to the conclusion that *tatar* is best considered a subspecies of this latter, a finding that confirms the allocation of similar specimens from Sulawesi to *R. euryotis* by Tate & Archbold (1939).

In view of the relatively small size of *R. e. tatar* it is of some interest to remark that Koopman (1982) has reported three specimens of *R. euryotis* from Kiriwina island, off eastern Papua New Guinea that are of similar size (Table 4), and one that is little larger (approaching *R. e. timidus*) from New Britain, but Smith & Hood (1981) have also recorded a much larger example from the same island. Koopman (1982) was inclined to doubt the validity of some at least of the subspecies of *R. euryotis* then recognised.

HIPPOSIDERIDAE

Hipposideros bicolor bicolor (Temminck, 1834)

Rhinolophus bicolor Temminck, 1834 : 19, pl. 1, fig. 3; 1835 : 18 (further description). Lectotype designated and type locality restricted to Anjer coast, northwestern Java by Tate (1941*a*).
Hipposideros javanicus Sody, 1937*a* : 215. Babakan, Kroja, Tjilatjap, central Java.

Specimen examined. W Java: ♀ Rijksmuseum van Natuurlijke Historie 29304 Tjilatjap (skin, skull; coll. 25 October 1929, apparently by H. J. V. Sody).

Remarks. This specimen appears to be one of those recorded by Sody (1930) as *H. galeritus longicauda* (Peters, 1861). However, the noseleaf lacks the lateral supplementary leaflets characteristic of *H. galeritus* and its allies and the specimen proves on further examination to represent *H. bicolor bicolor*. Dorsally, it is pale brown, the hairs with creamy or whitish bases that show through the darker tipping: the throat and chest are whitish, the remainder of the ventral surface brownish buff. The skull is elongate in outline, the rostrum and palate sharply tapered anteriorly; the narial swellings are only slightly inflated and there is a low sagittal crest; the zygomatic width is less than the mastoid width, the zygoma robust with low jugal eminence; the interparietal region is swollen and rather pronounced; the palation is shallowly V-shaped with wide mesopterygoid fossa; the sphenoidal bridge is wide, partially concealing elongate lateral apertures and there is a shallow oval sphenoidal depression; the cochlea are a little wider than their distance apart. The anterior upper premolar (pm^2) is very small, slightly extruded into a recess between the canine and the second upper premolar (pm^4); the posterior ridge of m^3 is about one half the length of the anterior ridge; the crown area of the outer lower incisors is very slightly greater than the crown area of the inner pair; anterior lower premolar (pm$_2$) threequarters the length and two thirds the height of the second lower premolar (pm$_4$) and two thirds its crown area.

Measurements: length of forearm 45·8; ear not measurable; length of tail c. 39; length of tibia c. 21; length of foot (c. u.) c. 8; greatest length of skull 19·0; condylobasal length 17·0; condylocanine length 16·8; basal length 14·6; palatal length 6·5; width across rostral swellings 4·8; least interorbital width 2·9; zygomatic width 9·3; width of braincase 8·7; mastoid width 9·6; c^1–c^1 (alveoli) 4·1; m^3–m^3 6·1; c–m^3 6·5; m$^{1-3}$ 4·0; length complete mandible from condyles 11·7; length right ramus from condyle 12·0; c–m$_3$ 7·0.

Discussion. This example agrees closely with the account by Tate (1941*a*) of the lectotype of *H. bicolor* (Temminck, 1834) in the Rijksmuseum van Natuurlijke Historie and with the description of *H. javanicus* by Sody (1937*a*), thought by Tate (loc. cit.) and by Hill (1963) to be a synonym of *bicolor*. Sody almost concurrently (1937*b*) recorded *javanicus* from the island of Banka: the specimen that he reports is slightly smaller in some respects either than the holotype of *javanicus* or the specimen of *bicolor* from Java reported here. There seems little doubt that *javanicus* must be considered a synonym of *H. b. bicolor*.

Hipposideros ater aruensis Gray, 1858

Hipposideros aruensis Gray, 1858 : 107. Aru Islands.

SPECIMENS EXAMINED. Papua New Guinea: ♀♀ BM(NH) 73.2036–2037 (both yg.) Kairiru Cave, near St Xavier's Mission, Kairiru I, near Wewak, East Sepik, c. 3° 21′ S, 143° 36′ E (in alcohol; coll. Aberdeen University Exploration Society Expedition to New Guinea, 1973); ♂ BM(NH) 80.612 S Tunnel, Bulolu Gorge, Wau, Morobe (in alcohol; coll. B. H. Gaskell, 'Operation Drake').

REMARKS. Little material is available from the more eastern part of the range of *H. ater* and for the present, following Hill (1963), specimens from New Guinea are referred to *H. a. aruensis.* McKean (1972) records specimens from Ambunti, Papua New Guinea. Length of forearm (BM(NH) 80.612) 40·9.

Hipposideros maggietaylorae erroris Smith & Hill, 1981

Hipposideros maggietaylorae erroris Smith & Hill, 1981 : 14. Yaguam Sulfur Cave, 5 miles S and 3 miles W of Madang, Madang Province, Papua New Guinea, 5° 17′ S, 145° 45′ E.

SPECIMENS EXAMINED. Papua New Guinea: 4 ♂♂ (2 yg.), 4 ♀♀ BM(NH) 73.2038–2045 Kairiru Cave, near St Xavier's Mission, Kairiru I, near Wewak, East Sepik, c. 3° 21′ S, 143° 36′ E (in alcohol; coll. Aberdeen University Exploration Society Expedition to New Guinea, 1973); ♀♀ (1 yg.) BM(NH) 75.1863–1865 St Xaviers, Kairiru I (in alcohol, skull of BM(NH) 75.1864 extracted; coll. A. M. Jones, Aberdeen University Exploration Society); ♂, ♀ BM(NH) 78.875–876 About 10 km S of Madang, 5° 15′ S, 145° 45′ E (in alcohol; coll. P. A. Morris); ♂, ♀♀ (1 yg.) BM(NH) 80.638–643 War Tunnel, Salamana, Morobe, 7° 03′ S, 147° 03′ E (in alcohol; coll. B. H. Gaskell, 'Operation Drake').

REMARKS. These specimens are listed by Smith & Hill (1981) in their account of *H. maggietaylorae*: those obtained by 'Operation Drake' are recorded erroneously as BM(NH) 80.516–522 (the suffixes in fact their collection numbers).

Hipposideros ridleyi Robinson & Kloss, 1911

Hipposideros ridleyi Robinson & Kloss, 1911 : 241 Botanic Gardens, Singapore.

SPECIMEN EXAMINED. Borneo: ♂ BM(NH) 82.160. Sepilok Forest Reserve, Sabah (in alcohol; coll. P. Zborowski).

REMARKS. This specimen is the first of *H. ridleyi* to be recorded from Borneo, the species being otherwise known from the type locality and from Selangor on the Malayan mainland (Medway, 1978). It may be easily recognised by its very large sub-triangular ears (length from meatus c. 21–23) broad noseleaf that lacks lateral supplementary leaflets, the expansion of the internarial septum to form a concave, saucer-like disc between and in front of the nostrils and by its high posterior leaf, the upper part supported by three septa defining four deep pockets. Length of forearm in the Bornean example 48·1, in the holotype (BM(NH) 61.329) 47·3 and in a specimen (BM(NH) 75.2000) from a locality between Kuala Kangsar and Rawang, Selangor, 48·5.

Hipposideros cervinus cervinus (Gould, 1863)

Rhinolophus cervinus Gould, 1863 : pl. 34, letterpress. 'Caves on Albany Island' (label on skin of holotype). Cape York, Queensland, Australia.

Specimens examined. C Sulawesi: 8 ♂♂, 5 ♀♀ BM(NH) 82.99–111 Taronggo, 1° 44′ S, 121° 40′ E; ♀♀ BM(NH) 82.112–113 R Ranu, 1° 51′ S, 121° 30′ E (all in alcohol, skulls of BM(NH) 82.100, 82.109–110, 82.112 extracted; coll. B. H. Gaskell, 'Operation Drake').

S Sulawesi: ♀♀ BM(NH) 82.114–115 Lalonggasu Meeto (Tomba Watu Cave), 18 km from Kendari Central (in alcohol, skull of BM(NH) 82.115 extracted; coll. B. H. Gaskell, 'Operation Drake').

Papua New Guinea: ♂♂ BM(NH) 75.1866–1867 Wageo I, Schouten Is, East Sepik; ♀ BM(NH) 75.1868 Kadovar I, Schouten Is; ♂, 3 ♀♀ BM(NH) 75.1869–1872 East Sepik (all in alcohol; coll. A. M. Jones, Aberdeen University Exploration Society); ♂ BM(NH) 76.386 Karkar I, Madang (in alcohol; coll. H. King); ♀ BM(NH) 78.877 About 10 km N of Baku, Gogol Valley, Madang, c 40 m (flat skin); 4 ♂♂, 7 ♀♀ BM(NH) 78.878–888 8 km W of Baku, c. 50 m; (in alcohol) (all coll. P. A. Morris); ♀♀ BM(NH) 80.607–611 N Tunnel, Bulolu Gorge, Wau, Morobe, 7° 19′ S, 146° 44′ E; ♂ BM(NH) 80.612 S Tunnel, Bulolu Gorge; ♂ BM(NH) Lae, Morobe, 6° 49′ S, 147° 03′ E; ♀♀ BM(NH) 80.614–617 Buso, Morobe, 7° 17′ S, 147° 08′ E; 6 ♂♂, 8 ♀♀ BM(NH) 80.618–631 Siboma, Morobe; 2 ♂♂, 4 ♀♀ BM(NH) 80.632–637 Coastal cave W of Kui Village, Morobe, 7° 22′ S, 147° 11′ E (all in alcohol; coll. B. H. Gaskell, 'Operation Drake').

New Hebrides: 2 ♂♂, 2 ♀♀ BM(NH) 73.1334–1337 Grotte Montmartre, Port Vila, Efate I, 20 m; 6 ♂♂, 3 ♀♀ BM(NH) 73.1338–1346 Mission Montmatre, Port Vila; 4 ♂♂, 2 ♀♀ BM(NH) 73.1347–1352 'Pig Cave', Harris Plantation, N coast Efate I, 40 m; ♂, ♀ BM(NH) 73.1353–1354 'Pig Cave', Narabut Camp, Efate I; 3 ♂♂, 3 ♀♀ BM(NH) 73.1355–1360 Lomboh Cave, Litzlitz, Port Stanley Bay, Malekula I, 5 m; ♂, 3 ♀♀ BM(NH) 73.1361–1364 Lipelip Cave, Amok, Malekula I, 440 m; 2 ♂♂, ♀ BM(NH) 73.1365–1367 Aouta Plantation, Aore I; ♂♂ BM(NH) 73.1368–1369 New Hebrides (all in alcohol. obtained by Earl of Cranbrook, Royal Society Expedition to the New Hebrides, 1973).

Remarks. Specimens from Sulawesi appear to be the first of *H. c. cervinus* to be recorded as such from that island, although earlier records of *H. galeritus galeritus* from Gimpoe or Bada and Peleng Island by Shamel (1940) and of *E. galeritus celebensis* from Talassa and Banti-moerang by Tate (1941*a*) may refer in fact to *cervinus.* A recent study at the British Museum (Natural History) by Jenkins & Hill (1981) has indicated that two species, namely *H. galeritus* Cantor, 1846 (including *insolens* Lyon, 1911 as a subspecies) and *H. cervinus* (including *labuanensis* Tomes, 1859*a* as a subspecies) occur in Borneo. *Hipposideros celebensis* Sody, 1936 based on specimens initially referred by this author (1930) to *H. galeritus galeritus,* has from the measurements given by Sody a broader braincase and shorter toothrow than the Sulawesian specimens here referred to *H. cervinus,* but Jenkins & Hill found two paratypes of *celebensis* to have longer toothrows and narrower zygomatic and braincase widths than Sody's measurements indicated. The paratypes unquestionably represent *H. cervinus* and these authors suggested from the available evidence that only *H. c. cervinus* occurs in Sulawesi, specimens from that island approaching the more easterly nominate subspecies rather than the geographically nearer Bornean subspecies *H. c. labuanensis.*

Measurements of specimens from Sulawesi: length of forearm (17) 45·0–49·1; condylocanine length (5) 14·3–14·9; width of rostrum (5) 4·9–5·1; least interorbital width (5) 2·5–2·8; zygomatic width (5) 8·8–9·1; width of braincase (5) 7·7–8·0; mastoid width (5) 8·6–8·9; c^1–c^1 (alveoli) (5) 3·7–3·9; m^3–m^3 (5) 6·0–6·1; c–m^3 (5) 5·8–6·0; length complete mandible from condyles (5) 10·3–10·8; length right ramus from condyle (5) 10·7–11·1; c–m_3 (5) 6·3–6·4.

Hipposideros diadema pullatus Andersen, 1905

Hipposideros diadema pullatus Andersen, 1905*c*: 498. Haveri, Papua New Guinea, 700 m.

Specimens examined. Papua New Guinea: ♂ BM(NH) 78.889 (flat skin), ♀,♂ 78.890–891 (in alcohol) About 10 km S of Madang (coll. P. A. Morris).

Hipposideros dinops pelingensis Shamel, 1940

Hipposideros pelingensis Shamel, 1940 : 353. Peling (= Peleng) I. E of Sulawesi.

Specimens obtained. S Sulawesi: ♂, 2 ♀♀ BM(NH) 82.116–118 Lalonggasu Meeto (Tomba Watu Cave), 18 km from Kendari Central (in alcohol, skulls of BM(NH) 82.117–118 extracted; coll. B. H. Gaskell, 'Operation Drake').

Remarks. Shamel (1940) diagnosed *pelingensis* solely on the basis of its shorter tibia (length 38·2–41·0) when compared with *H. dinops* Andersen, 1905*c* from the Solomon Islands. Tate (1941*a* : 376) recorded *pelingensis* from Talassa, (Maros), south Sulawesi, listing (p. 391) the specimens as *H. diadema pelingensis* although (p. 376) comparing and associating *pelingensis* with *dinops*. Hill (1963) considered *pelingensis* a subspecies of *H. dinops* but had seen no examples of the Sulawesian form.

These specimens agree favourably in size and structure with the nominate subspecies from the Solomon Islands but the rostrum is very slightly narrower, the upper canines a little smaller at the base and the toothrows a little shorter. However, in most of these features they closely resemble the smallest of the available specimens from the Solomons, an example (BM(NH) 67.2118) from Malaita Island reported by Hill (1971*a*) who gave measurements of *H. d. dinops* and discussed variation in this subspecies.

External measurements: length of forearm (3) 93·4–96·9; length of tibia (3) 39·9–40·9. Cranial measurements (♂ BM(NH) 82.117, ♀ 82.118): greatest length of skull 36·5, 36·0; condylobasal length 32·4, 32·4; condylocanine length 31·5, 31·4; palatal length 13·2, 13·0; rostral width 10·2, 9·9; anteorbital width 10·0, 9·0; length of anterorbital foramen 2·8, 2·7; width of anteorbital foramen 0·7, 0·8; least interorbital width 3·6, 3·9; zygomatic width 20·8, 20·2; width of braincase 13·9, 13·7; mastoid width 16·7, 16·1; c^1–c^1 (alveoli) 9·3, 8·9; m^3–m^3 12·7, 12·7; c–m^3 13·8, 13·4; length c^1 4·12, 3·97; width c^1 2·83, 2·85; length complete mandible from condyles 24·7, 24·5; length right ramus from condyle 25·5, 25·4; top of condyle–tip of angular process 5·8, 6·1; bottom of condyle–tip of coronoid process 7·2, 7·6; tip of angular process–tip of coronoid process 10·9, 11·7; c–m_3 15·6, 14·9.

Discussion. Specimens of *H. d. pelingensis* are of particular interest in connection with the very large *H. inexpectatus* Laurie & Hill, 1954, no material of *pelingensis* being available in London when this was described. Direct comparison shows *pelingensis* to be considerably smaller, with lower, narrower rostrum, much less developed sagittal and lambdoidal crests, less expanded zygomata and much smaller teeth. There is especially a great contrast in the large and heavy mandible of *inexpectatus* and the relatively lighter and by comparison apparently delicate mandible of *pelingensis*. Until recently *H. inexpectatus* was known in the literature solely from its holotype (BM(NH) 25.6.5.19) from Poso, north Sulawesi but Fieler (1981) has reported two further examples, from Gorontalo and Minahassa. They are specimens that have been for many years in the collections of the Staatliches Museum für Tierkunde in Dresden, formerly identified as *H. diadema* (Geoffroy, 1813).

Aselliscus tricuspidatus novehebridensis Sanborn & Nicholson, 1950

Aselliscus tricuspidatus novehebridensis Sanborn & Nicholson, 1950 : 461. Cave on Segond Channel, Espiritu Santo I, New Hebrides.

Specimens examined. New Hebrides: 15 ♂♂, 8 ♀♀ BM(NH) 73.1370–1392 Aouta, Aore I; 2 ♂♂, 2 ♀♀ BM(NH) 73.1393–1396 Aouta Plantation, Aore I; ♂, ♀ BM(NH) 73.1397–1398 Hog Harbour, Espiritu Santo I, 150 ft; 3 ♂♂, 2 ♀♀ BM(NH) 73.1399–1403 Senwar Cave, Tenmial, NW coast of Malekula I, 40 m (BM(NH) 73.1393, 73.1396 skins, skulls, all others in alcohol; obtained Earl of Cranbrook, Royal Society Expedition to the New Hebrides, 1971).

Remarks. In size (length of forearm 39·8–43·5) these specimens agree with *A. t. novehebridensis* as described by Sanborn & Nicholson (1950) and, indeed, extend the range of forearm length given by these authors. They are generally larger than specimens from the Solomon Islands referred to *A. t. tricuspidatus* (Temminck, 1834) by Hill (1956, 1971*a*) or others from islands in the same group reported by Sanborn & Beecher (1947).

External measurements: length of forearm (20 ♂♂) 39·8–42·2 (41·2), (14 ♀♀) 40·3–43·5 (42·0). Cranial measurements (♂ BM(NH) 73.1396, ♀ 73.1393): greatest length of skull 15·5, 15·7; condylobasal length 13·6, 14·0; condylocanine length 13·2, 13·6; palatal length 2·6, 2·7; rostral width 4·9, 5·0; least interorbital width 1·7, 1·7; zygomatic width 7·9, 7·8; width of braincase 6·1, 6·0; mastoid width 7·1, 7·1; c^1–c^1 (alveoli) 4·0, 3·9; m^3–m^3 5·5, 5·5; c–m^3 5·7, 5·7; length complete mandible from condyles 9·8, 10·0; length right ramus from condyle 10·0, 10·2; c–m_3 6·0, 6·1.

Aselliscus tricuspidatus (Temminck, 1834)

Rhinolophus tricuspidatus Temminck, 1834 : 20, pl. 1, fig. 4. Amboina I, Molucca Is.

SPECIMEN EXAMINED. Papua New Guinea: ♂ BM(NH) 78.892 (yg.) 8 km E of Baku, Gogol Valley, Madang, 50 m (in alcohol; coll. P. A. Morris).

REMARKS. No attempt has been made to allocate this young specimen to subspecies: in any event little comparative material from New Guinea is available in the collection of the British Museum (Natural History). There is however a substantial representation from the Moluccan islands of Buru and Ceram and from Batchian Island, the Kei Islands, and the Solomon Islands. These are smaller (length of forearm (99) 47·2–42·0; condylocanine length (37) 12·1–13·0; palatal length (43) 2·1–2·5; zygomatic width (41) 6·6–7·3; width of braincase (44) 5·4–5·9; mastoid width (44) 6·3–6·9; c^1–c^1 (alveoli) (45) 3·1–3·7; m^3–m^3 (48) 4·6–5·2; c–m^3 (52) 5·0–5·4) than *A. t. novehebridensis* and are referred to *A. t. tricuspidatus*. According to Koopman (1982), similarly small specimens are found on the east Papuan islands. Specimens reported from Papua New Guinea by McKean (1972) and from West Irian by Koopman (1982), however, are larger and tend to bridge the size differences between *tricuspidatus* and *novehebridensis* or to approach the latter.

Coelops robinsoni Bonhote, 1908

Coelops robinsoni Bonhote, 1908 : 4. Foot of Mt. Tahan, Pahang, Malaya.

SPECIMEN EXAMINED. Borneo: ♂ BM(NH) 79.1398 Deer Cave, Gunung Mulu National Park, Sarawak (partially mummified, now in alcohol, skull extracted; found S. Proctor, Royal Geographical Society Expedition to Gunung Mulu, 1977–78).

REMARKS. The small leaf-nosed bat *C. robinsoni* is known from two specimens from Malaya, one the holotype (BM(NH) 6.10.4.9) in the British Museum (Natural History), the other (USNM 175000) from Port Swettenham, in the United States National Museum of Natural History, and from a specimen from Teratau Island, off southern Thailand, reported by Chasen (1940). The species was reviewed in some detail by Hill (1972) who pointed out that two specimens referred to *C. robinsoni* by Robinson & Kloss (1915*b*) are in fact *C. frithii*. This Bornean specimen agrees closely with the holotype of *C. robinsoni* but has a very slightly wider skull. The discovery of the species in Borneo perhaps adds some weight to the suggestion by Hill (1972) that *C. hirsuta* (Miller, 1910) from Mindoro Island in the Philippines is closely allied to *C. robinsoni*, which indeed it may represent. Unfortunately, it is so far known only from the holotype skin.

Measurements of BM(NH) 79.1398: length of forearm 36·5; greatest length of skull to canine 14·6; condylocanine length 12·7; rostral width 3·9; least interorbital width 1·9; zygomatic width —; width of braincase —; mastoid width —; c^1–c^1 (alveoli) 3·2; m^3–m^3 5·0; c–m^3 5·0; length complete mandible from condyles 8·6; length right ramus from condyle 8·8; c–m_3 5·5.

VESPERTILIONIDAE

VESPERTILIONINAE

Myotis muricola (?) browni Taylor, 1934

Myotis browni Taylor, 1934 : 288. Near Saub, Cotobato, Mindanao I, Philippine Is.

Specimens examined. C Sulawesi: ♂, 4 ♀♀ BM(NH) 82.119–123 R Ranu, 1° 51′ S, 121° 30′ E (in alcohol, all skulls extracted; coll. B. H. Gaskell, 'Operation Drake').

Remarks. These small examples are referred provisionally to *browni*, a small representative of *M. muricola* similar in size to *M. m. caliginosus* (Tomes, 1859) from the southern Himalaya or to *M. m. niasensis* Lyon, 1916 from Nias Island, off west Sumatra. Further material from the Philippines and Sulawesi might lead to the recognition of a Sulawesian subspecies: certainly as represented by these specimens from the Ranu River members of the Sulawesian population are considerably smaller than others of *M. muricola* from Thailand, Malaya, Borneo, Java, the Lesser Sunda Islands, and Amboina. There appears to be no previous record of *M. muricola* as such from Sulawesi.

Measurements of five specimens, except where indicated: length of forearm: 31·4–32·7; greatest length of skull 12·3–13·0; condylobasal length 11·8–12·6; condylocanine length 11·2–12·0; least interorbital width 2·8–3·0; zygomatic width (3) 7·8–8·0; width of braincase 5·9–6·0; c^1–c^1 (alveoli) (5) 3·2; m^3–m^3 5·1–5·4; i^2–m^3 5·4–5·8; c–m^3 4·9–5·3; length complete mandible from condyles 8·8–9·5; length right ramus from condyle 9·0–9·6; c–m_3 5·4–5·8.

Discussion. There is some confusion over the correct name for small *Myotis* with small feet (subgenus *Selysius*) occurring in Indo-Australia, the issue apparently turning on the species to be found in the northern part of the Indian sub-continent. Numerous names have been applied to these small bats with forearm 30–36 in length and with pm$^3_3$ reduced but not intruded or only slightly intruded from the toothrows: the major question is whether or not these should be associated with the otherwise Palaearctic species *M. mystacinus* (Kuhl, 1819) or should be considered a distinct species *M. muricola* (Gray, 1846). Indo-Australian names involved are:

Vespertilio muricola Hodgson, 1841 (nom. nud.)	
Vespertilio muricola Gray, 1846	Nepal
Vespertilio siligorensis Horsfield, 1855	Nepal
Vespertilio darjelingensis Horsfield, 1855	
Vespertilio (Pternopterus) lobipes Peters, 1867*b*	Burma
Vespertilio caliginosus Tomes, 1859*b*	India
Vespertilio nipalensis Dobson, 1871*b*	Nepal
Vespertilio blanfordi Dobson, 1871*b*	Himalayas
Vespertilio moupinensis Milne Edwards, 1872	Szechuan
Myotis niasensis Lyon, 1916	Nias I
Myotis meinertzhageni Thomas, 1926	Kashmir
(?) *Myotis latirostris* Kishida, 1932	Taiwan
Myotis browni Taylor, 1934	Mindanao I, Philippine Is.
Myotis herrei Taylor, 1934	Luzon I, Philippine Is.
Myotis muricola orii Kuroda, 1935	Taiwan

Thomas (1915*a*) divided *M. muricola* from a *mystacinus* group on account of its allegedly broader, more solidly built skull, heavier teeth, especially the canines, and the greater intrusion of the posterior of the two small premolars (pm$^3_3$). According to this author, *M. muricola* included *lobipes*, while his *mystacinus* group included *caliginosus*, *blanfordi*, *nipalensis, siligorensis* and *darjelingensis*. Thomas recognised two 'forms' within the *mystacinus* group, one with low braincase and canines of normal size to include *caliginosus*, with synonyms *blanfordi* and perhaps *nipalensis*, the other with a high crown and reduced canines to include *siligorensis* and its synonym *darjelingensis*. *Myotis siligorensis* is today recognised as a distinct and valid species.

The entire question was reviewed in some detail by Tate (1941*d*) who was unable to make any certain application of the names that he discussed beyond recognising (p. 543) *muricola* (=*moupinensis*), *caliginosus* (=*blanfordi*) and *nipalensis* (=*meinertzhageni*) as subspecies of *M. mystacinus*, with *siligorensis* a valid species in its own right. Elsewhere (p. 545) Tate considered *herrei* and *browni* probably related to *niasensis* which he thought to be a subspecies of *M. mystacinus*, with the suggestion that *lobipes* may also represent this species. Finally, Tate (p. 564) remarked that he did not believe *muricola* to be the correct subspecific name for any East Indian representative and suggested that all should be referred to *M. mystacinus*: specimens from Sumatra, Java and Borneo he allocated to *niasensis* with the proviso that this might be a synonym of *lobipes*, presumably intending that they should be called *M. mystacinus niasensis*.

Chasen (1940) called most Sundanesian specimens *M. muricola muricola* but employed *niasensis* as a valid subspecies of *M. muricola* for those from Nias Island, while Laurie & Hill (1954) followed the lead given by Tate (1941*d*) in employing *M. mystacinus* but used *muricola* as the subspecific name for specimens from the Lesser Sunda Islands, and, by implication, from much of Sundanesia. Findley (1972) recognised *mystacinus* and *muricola* groups within *Selysius* and considered these forms unlikely to be conspecific as once was thought since Tate (1941*d*) had recorded them sympatrically in Nepal, apparently through a reference to Scully (1887) who reported '*mystacinus*' from that country (later described as *siligorensis*) although in fact Tate listed *muricola* as a subspecies of *mystacinus*. Findley included *meinertzhageni* in *mystacinus* and *caliginosus, blanfordi* and *moupinensis* in *muricola*, with the suggestion that *muricola* also includes the various populations of tropical Asia, having associated *browni, latirostris* and *niasensis* (inter alia) with his *muricola* group. More recently, Corbet (1978) has excluded all but *meinertzhageni* among the Indian forms from any discussion of *M. mystacinus*, considering *muricola* specifically distinct.

The collections of the British Museum (Natural History) indicate that two distinctively coloured *Myotis* (excluding *siligorensis*) occur in the northern part of the Indian subcontinent, although cranially they are very similar. One of these is exemplified by a small series of specimens (BM(NH) 16.7.29. 37–41, 16.7.28.90, part of those reported as *muricola* by Wroughton, 1917) from Hasimara Tea Estate, E bank of Toorsa River, c. 8 miles from Bhutan Hills, Jalpaiguri District, Bhutan Duars, 500–600 ft, c. 26° 50′ N, 89° 20′ E. These are brownish dorsally, the hairs black or blackish brown at the base and for most of their length, tipped with shiny, paler ochraceous brown. Ventrally the specimens are whitish, the hairs black based, tipped with white or creamy white, the black undercolour showing through to a limited extent. The collections also include a similar specimen (BM(NH) 9.7.27.3) from Sirguffara, Kashmir, 6000 ft in which the white ventral tipping is a little less evident, and a further example (BM(NH) 23.9.1.12), reported by Lindsay (1926) as *muricola*, from Chirot, in the Pattan Valley, Lahul, near the junction of Chandra and Bhaga Rivers, 9800 ft with the dorsal pelage more heavily tipped with burnished ochraceous. A specimen (BM(NH) 71.13) in alcohol, from Kokernag, Kashmir evidently also has brownish dorsal pelage and whitish underparts. These specimens clearly represent *M. mystacinus* and agree closely with the description of *M. mystacinus nipalensis* by Dobson (1871*b*) to which they are referred.

Specimens of this type appear to have been the basis of the remark by Allen & Coolidge (1940) that *muricola* of the Nepal–Himalaya foothills has the dorsal pelage tipped with shiny-ochraceous rather than duller brown, with a whitish rather than yellowish ventral surface. Thus in contrasting such specimens with East Indian examples they apparently compared their more eastern specimens with *M. mystacinus* rather than with *muricola* as they assumed. Tate (1941*d*) quotes these authors in support of the distinctiveness of supposed Himalayan *muricola*: possibly their comment influenced his opinion that *muricola* should not be applied as a subspecific name to any East Indian form.

Tate (1941*d*) and Corbet (1978) suggested that *meinertzhageni* might be synonymous with *nipalensis*, Ellerman & Morrison-Scott (1951) in fact listing it as a provisional synonym of *nipalensis*. However, the holotype BM(NH) 26.3.1.1 of *meinertzhageni* is considerably paler dorsally than the specimens here referred to *nipalensis*, the pelage heavily tipped with creamy white, faintly tinged with ochraceous, the ventral surface with pelage that is white tipped over a black base.

The collections also include further specimens (BM(NH) 23.9.1.13–14, identified as *caliginosus* by Lindsay, 1926) from Samayala, in the Kangra Valley, that evidently represent a smaller, darker form than *M. mystacinus*, its dorsal pelage darker and blacker, less profusely tipped with shiny brown, its ventral pelage tipped with ochraceous brown rather than with whitish, although both dorsally and ventrally the hairs are blackish at the base. Similar dark-bellied specimens in the collections come from other localities in the Punjab (BM(NH) 7.11.21.4, 10.1.18.17–18), Sikkim (BM(NH) 91.10.7.57, 15.9.1.21), Kashmir (BM(NH) 8.7.6.10) and Pakistan (from Murree Hills) (BM(NH) 71.1570–1573) at altitudes from 6500–7600 ft: the highest at which these are represented is by a specimen (BM(NH) 14.7.10.55) from the Pindar Valley at 10 700 ft. All of these specimens agree closely with *caliginosus* or with *blanfordi* which is evidently a synonym of *caliginosus*: in turn this last is similar to but slightly larger than *muricola*. There seems little doubt that these are conspecific and that *M. muricola caliginosus* is the westernmost representative of *M. muricola*, overlapping in parts of its range with *M. mystacinus nipalensis*.

Further east, specimens of *muricola* from Nepal, in wet preservation, have the characteristically dark ventral surface of *caliginosus*, lacking any white tipping. Dry examples from Thailand, Vietnam, Borneo and Java have a brownish dorsal surface similar to that of *caliginosus*, the hairs blackish brown at the base and tipped with ochraceous brown. The ventral surface is buffy brown to greyish black, the hairs having dark bases with buffy brown or greyish buff tips, but often with much of the darker undercolour showing through the paler tipping. Lack of mainland material prevents any proper assessment of possible subspecific variation: as Chasen (1940) pointed out the pattern of size variation in Malaya, Sumatra, Borneo and Java throws doubt on the necessity of recognising more than one Sundanesian subspecies. For the present, therefore, I refer specimens from this area and its many islands except Nias to one subspecies, *M. muricola muricola*. *Myotis niasensis* Lyon, 1916 is very small and may well justify distinction as *M. muricola niasensis*, while the Philippine forms *herrei* and *browni* also seem separable on similar grounds, together with small examples from Sulawesi.

No attempt has been made in this brief survey to discuss named forms occurring outside the Indo-Australian region, or to examine the relationship of *M. muricola* to any of the other Palaearctic forms now recognised. This question is briefly reviewed by Corbet (1978).

Myotis ater (Peters, 1866)

Vespertilio ater Peters, 1866*a* : 18. Ternate I.
Vespertilio adversus var. *amboinensis* Peters, 1866*b* : 400. Amboina I, Molucca Is.
(?) *Vespertilio australis* Dobson, 1878 : 317. New South Wales, Australia.

Specimens examined. C Sulawesi: ♂ BM(NH) 82.124 R Ranu, 1° 51′ S, 121° 30′ E (in alcohol, skull extracted; coll. B. H. Gaskell, 'Operation Drake').

Siberut I. Mentawei Is: 2 ♂♂ (1 yg.). 3 ♀♀ BM(NH) 78.2932–2936 Headquarters of Sirimuri R, off Saibi R (in alcohol, skulls of BM(NH) 78.2933–2934 extracted; coll. J. J. Whitten).

Remarks. Although similar to *M. muricola*, *M. ater* is larger, with a heavier, wider rostrum and more inflated braincase; pm^3 is small, intruded from the toothrow while pm_3 is slightly intruded, squashed between pm_2 and pm_4. As Tate (1941*d*) correctly pointed out, pm_2 is less reduced in *ater (amboinensis)* than in *muricola* and its allies. This specimen complements others (BM(NH) 97.1.12.48–51, 7.1.1.504, 7.1.1.507) in the collections in London from Sulawesi: Shamel (1940) and Tate (1941*d*) recorded (as *amboinensis*) specimens from several Sulawesian localities to which Tate adds Vagian and Peleng Islands, and Papua New Guinea.

Measurements of BM(NH) 82.124, with those of other Sulawesian specimens in parentheses: length of forearm 36·5 ((6) 36·1–38·4); greatest length of skull 13·9 (14·2, 14·4); condylobasal length 13·3, (13·5, 13·7); condylocanine length 12·6 (12·8, 13·1); least interorbital width 3·5 (3·4, 3·5); zygomatic width 8·7 (—); width of braincase 6·4 (6·9); mastoid width 7·0 (7·6); c^1–c^1 (alveoli) 3·6 ((6) 3·8–4·0); m^3–m^3 5·6 ((5) 5·9–6·2); i^2–m^3 6·5 ((6) 6·6–6·8); c–m^3 5·4 ((6) 5·6–5·7); length complete mandible from condyles 10·4 ((3) 10·4–10·7); length right ramus from condyle 10·7 ((6) 20·7–10·9); c–m_3 5·8 ((6) 5·9–6·1.

Specimens from Siberut Island in the Mentawei Islands whence *M. ater* has not before been recorded agree in structure and size with *M. ater* from Sulawesi and the Molucca Islands, except that pm^3_3 are a little less reduced and less sharply intruded from the toothrows. Measurements of Siberut specimens: length of forearm (4) 34·8–36·2; greatest length of skull 14·1, 14·3; condylobasal length 13·5, 13·6; condylocanine length 12·9, 12·9; least interorbital width 3·5, 3·6; zygomatic width 9·3, 9·2; width of braincase 6·6, 6·5; mastoid width 7·5, 7·5; c^1–c^1 (alveoli) 3·9, 3·9; m^3–m^3 6·0, 6·2; i^2–m^3 6·6, 6·6; c–m^3 5·6, 5·6; length complete mandible from condyles 10·4, 10·5; length right ramus from condyle 10·9, 10·9; c–m_3 6·0, 5·9.

DISCUSSION. Thomas (1915*a*) considered *M. ater* to be a larger ally of *M. muricola* from Sulawesi and the Moluccan Islands of Amboina, Buru and Ceram. Tate (1941*d*) retained *ater* in a distinct section of the subgenus *Selysius* (p. 545) although he also indicated (p. 564) that *ater,* as *amboinensis* with which Tate thought it possibly synonymous, might be a subspecies of *M. mystacinus* (=*M. muricola* in the present sense). Laurie & Hill (1954) listed *ater* as a subspecies of *M. mystacinus* (=*M. muricola*): however, specimens from the Ranu River show the two forms to occur sympatrically in Sulawesi. Moreover, a small specimen (BM(NH) 80.1.17.3) from Amboina (length of forearm 34·3, condylobasal length 12·9, condylocanine length 12·3, c–m^3 5·2) with small pm_2 and pm^3_3 slightly intruded does not represent *ambionensis* of Peters (length of forearm 37·5) but instead is referable to *M. muricola.* Although the collections in London contain no example of *ater (amboinensis)* from Amboina, specimens from Buru (BM(NH) 10.3.3.28–30, 23.1.1.14) and Ceram (BM(NH) 10.3.4.32–43, 23.1.2.15) are large (length of forearm (16) 36·8–39·2, condylobasal length (11) 13·7–14·1, condylocanine length (11) 13·0–13·5, c–m^3 (11) 5·6–5·9) and represent this species.

Hill (1962) and Medway (1965, 1977) regarded *ater* and *muricola* as conspecific, treating both as subspecies of *M. mystacinus* (=*M. muricola* in the present sense). The former of these authors provisionally associated *nugax* Allen & Coolidge, 1940 from northern Borneo and Culion Island in the Philippines (Sanborn, 1952) with *M. mystacinus* (=*M. muricola*) as a possible subspecies, while the latter considered it to be the subspecies of *M. mystacinus* (=*M. muricola*) in the highlands of northwestern Borneo, with *M. m. muricola* in the lowlands. However, on description and size it appears to represent *M. ater* and it is possible that the two may be conspecific as Tate (1941*d*) suggested, but the length of the toothrow of *nugax* given by Allen & Coolidge is rather large for *ater.* Tate (1941*d*) considered that these authors apparently had included the incisors rather than measuring from the canine as is customary and gave for MCZ 36075 (the holotype is MCZ 36076) in the Museum of Comparative Zoology, Harvard, a value for i^2–m^3 of 6·5 and for c–m^3 of 5·5, closely corresponding to *M. ater.*

Although similar in numerous points of size to *M. abbotti* Lyon, 1916 from North Pagi Island in the Mentawei Islands, specimens of *M. ater* from Siberut quite clearly show no relation to that form. Comparison with the account by Lyon indicates that the interorbital region and braincase of *abbotti* are considerably wider: moreover, Tate (1941*d*) considered *abbotti* to belong to the subgenus *Leuconoe* rather than to *Selysius,* although Lyon originally described it as a subspecies of *M. muricola.* Tate in fact thought it belonged with *M. adversus* Horsfield, 1824, possibly as a synonym of *M. a. carimatae* Miller, 1906*d.* Diagnostic features not mentioned by Lyon can be gleaned from Shamel (1942) who noted that the wing membrane is attached to the ankle, thus differing from *M. ater* and from *M. horsfieldii* in which it is attached to the metatarsus, that pm^3 is much smaller than pm^2, its tip only slightly above the cingulum of the latter tooth, crowded completely from the toothrow with pm^2 and pm^4 almost in contact, while pm_3 is in the toothrow but crowded slightly to the inside. These features suggest alliance to *M. hasseltii* (Temminck, 1840) of which the nominate subspecies occurs in Java, Sumatra and Malaya, *M. h. continentis* Shamel, 1942 in Thailand and Burma and *M. h. macellus* (Temminck, 1840) in Borneo. Specimens apparently referable to *M. hasseltii* have also been obtained in Sri Lanka (Hill, 1976*a*).

The status of *Vespertilio australis* Dobson, 1878, allegedly from New South Wales, Australia has remained in doubt for many years. However, McKean (1970) has reproduced a detailed letter from Dr A. M. Husson describing its holotype, housed in the Rijksmuseum van Natuurlijke Historie, Leiden. The description, especially of the dentition, and the measurements that Dr Husson has provided agree closely with *M. ater.* Measurements given for the holotype of *australis,* with comparable values for *ater* from Sulawesi and the Moluccas in parentheses: length of forearm (ex Dobson, who gives 1′ 55′′) 39·5 ((23) 36·1–39·2); interorbital width 3·9 ((14) 3·3–3·5); c^1–c^1 3·7 ((18) 3·6–4·3); i^2–m^3 6·9 ((18) 6·5–7·1); c–m^3 5·8 ((18) 5·4–5·9); i_1–m_3 7·0 ((15) 6·9–7·5), c–m_3 6·3 ((18) 5·8–6·3.

Dr Husson rejects any relationship between *australis* and *M. adversus* but suggests instead that on dental features *australis* might be allied to *M. muricola*: to this McKean added that Laurie & Hill (1954) considered this a subspecies of *M. mystacinus* with the further subspecies *M. mystacinus ater* extending to Papua. The available evidence suggests strongly that *australis* is at least conspecific with *M. ater* but the origins of the holotype and only known specimen are obscure. Although it is on a mount marked 'Sydney N. Hollande' it may have been mislabelled, collected elsewhere, or may be a ship-assisted vagrant as Allison (1980) suggested.

Myotis horsfieldii horsfieldii (Temminck, 1840)

Vespertilio horsfieldii Temminck, 1840 : 226. Java.
Leuconoe lepidus Thomas, 1915*d* : 171. Baram, Sarawak, Borneo.

Specimens examined. C Sulawesi: ♂, 5 ♀♀ BM(NH) 82.125–130 Taronggo, 1° 44′ S, 121° 40′ E (in alcohol, skulls extracted; coll. B. H. Gaskell, 'Operation Drake').

Remarks. Specimens from Sulawesi are cranially a little larger in some respects than those from Thailand (*M. h. deignani* Shamel, 1942) or Malaya, Borneo and Java (*M. h. horsfieldii*; the Bornean form *lepidus* was considered only weakly if at all separable by Hill (1974) and Medway (1977) has since synonymised it with the nominate subspecies), but the differences are very slight. Measurements appear in Table 5.

Discussion. *Myotis horsfieldii* was first recorded as such from Sulawesi by Hill (1974) who reported a specimen (BM(NH) 73.1804) from Wawondula in the southern part of the island. Subsequently Jones & Maa (1976) reported an individual from Makassar (5° 07′ S, 119° 24′ E) as *M. horsfieldii* with the comment that Jentink (1883) had listed this species from northern but not southern Sulawesi and that Laurie & Hill (1954) had listed it from Peleng Island. However, neither Jentink nor Laurie & Hill mention *M. horsfieldii* but instead report *M. adversus* (the record in Laurie & Hill was drawn from Tate (1941*d*) who also reported *adversus* from Menado in northern Sulawesi) so that the exact identity of the specimen in the United States National Museum of Natural History reported by Jones & Maa must remain uncertain.

Table 5 Measurements of *Myotis horsfieldii* (numbers of specimens examined in parentheses).

	M. h. *deignani* Thailand	*M. h.* *horsfieldii* Malaya	*M. h.* *horsfieldii* Java	*M. h.* *horsfieldii* Borneo	*M. h.* *horsfieldii* Sulawesi	*M. h.* (?) *peshwa* India	*M. h.* (?) *dryas* S Andaman I
Length of forearm	36·3, 35·4	(5) 36·4–38·7	(29) 35·2–40·0	(9) 36·3–38·2	(7) 37·1–38·2	(8) 36·3–40·1	37·4, 35·3
Greatest length of skull	15·1, 15·3	(4) 15·2–15·9	(18) 14·6–16·0	(3) 15·7–15·8	(7) 15·1–15·8	(8) 15·4–16·1	15·2, —
Condylobasal length	13·9, 14·1	(4) 13·7–14·3	(18) 13·2–14·7	(3) 14·3–14·7	(7) 14·2–14·8	(8) 14·3–14·7	14·7, —
Condylocanine length	13·5, 13·6	(4) 13·1–13·6	(18) 13·0–13·9	(3) 13·5–13·8	(7) 13·5–14·3	(8) 13·6–14·1	13·5, —
Least interorbital width	3·5, 3·5	(4) 3·4–3·6	(18) 3·2–3·7	(3) 3·5–3·6	(7) 3·5–3·8	(8) 3·5–3·9	3·7, —
Zygomatic width	—, —	9·3, 9·4	9·4, 9·5	9·0	(7) 9·3–9·9	(3) 9·7–9·8	9·4, —
Width of braincase	7·1, 7·3	(4) 6·9–7·3	(18) 6·9–7·3	(3) 7·1–7·3	(7) 7·3–7·8	(8) 7·3–7·5	7·2, —
Mastoid width	7·7, 7·7	(4) 7·5–7·9	(17) 7·5–8·0	(3) 7·5–7·9	(7) 7·7–8·0	(8) 7·9–8·2	7·8, —
c^1–c^1 (alveoli)	4·2, 4·2	(3) 4·2–4·3	(18) 3·9–4·3	(3) 4·2–4·3	(7) 4·2–4·4	(8) 4·0–4·3	4·2, —
m^3–m^3	6·0, 5·8	(4) 5·7–6·1	(18) 5·6–6·1	5·9, 6·1	(7) 6·0–6·2	(8) 5·8–6·1	5·9, —
c–m^3	5·7, 5·7	(4) 5·6–5·9	(18) 5·4–5·8	(3) 5·8–6·0	(7) 5·7–6·0	(8) 5·5–5·8	5·7, 5·6
Length complete mandible from condyles	10·5, 10·5	10·9, 10·8	(16) 10·4–11·0	10·8, 11·0	(7) 10·6–11·2	(8) 10·6–11·0	10·7, —
Length right ramus from condyle	10·9, 10·9	(4) 10·9–11·3	(18) 10·8–11·5	11·2	(7) 10·9–11·5	(8) 11·1–11·5	11·1, —
c–m_3	6·1, 6·1	(4) 6·0–6·3	(18) 6·0–6·4	(3) 6·2–6·4	(7) 6·2–6·5	(8) 6·1–6·3	6·0, —

Table 6 Measurements of *Myotis hasseltii* (number of specimens examined in parentheses).

	M. h. continentis Burma	*M. h. continentis* Thailand, Cambodia	*M. h. hasseltii* Malay Peninsula, Java	*M. h. macellus* Borneo	*M. h.* (?) Sri Lanka
Length of forearm	38·5	(12) 35·7–39·2	(8) 38·8–41·2	36·9	(5) 37·4–40·3
Greatest length of skull	16·2	(8) 15·3–16·0	(6) 15·6–16·3	15·4	(4) 16·0–16·6
Condylobasal length	15·1	(8) 14·0–14·6	(5) 14·2–15·0	14·1	(4) 14·8–15·5
Condylocanine length	14·3	(8) 13·3–13·8	(5) 13·5–14·3	13·4	(4) 14·2–14·7
Least interorbital width	4·2	(10) 3·9–4·2	(7) 3·7–4·2	3·9	(4) 4·0–4·2
Zygomatic width	—	(5) 9·9–10·2	10·3	—	—
Width of braincase	8·1	(9) 7·5–7·9	(7) 7·6–8·1	7·8	(4) 8·1–8·6
Mastoid width	8·5	(8) 8·0–8·6	(5) 8·0–8·7	8·0	(4) 8·6–8·7
c^1–c^1 (alveoli)	4·6	(8) 4·2–4·5	(6) 4·1–4·6	4·3	(4) 4·4–4·6
m^3–m^3	6·5	(9) 5·8–6·2	(7) 6·1–6·7	6·2	(4) 6·5–6·7
c–m^3	6·1	(9) 5·3–5·7	(7) 5·7–6·1	5·6	(4) 5·9–6·0
Length complete mandible from condyles	—	(8) 10·5–11·4	(4) 10·8–11·3	10·8	(4) 11·2–11·6
Length right ramus from condyle	11·8	(5) 10·3–11·1	(7) 11·1–11·8	11·0	(4) 11·6–12·0
c–m_3	6·4	(9) 5·9–6·2	(7) 6·1–6·5	6·1	(4) 6·3–6·5

Hill (1976*a*) thought *peshwa* Thomas, 1915*a* from India and *dryas* Andersen, 1907*b* closely related to *M. horsfieldii* of which both are here considered provisional subspecies. It is also possible that *M. jeannei* Taylor, 1934 from Zamboanga Island, Philippine Islands may represent *M. horsfieldii*: there is reasonable agreement in size and the wing membrane in *jeannei* is attached to the foot about halfway between the heel and the base of the toe, a characteristic feature of *M. horsfieldii* when compared with *M. adversus* or *M. hasseltii* in which it attached at the end of the tibia or at the ankle.

Myotis hasseltii continentis Shamel, 1942

Myotis adversus continentis Shamel, 1942 : 323. Bangkok, Thailand.

Specimen examined. Burma: ♂ BM(NH) 78.154 British Embassy Residence compound, Rangoon (in alcohol, skull extracted; coll. D. W. & G. Walton).

Remarks. This specimen is the first of *M. hasseltii* to be reported from Burma, although the species is known to occur farther north in Thailand, at Chiangmai (BM(NH) 9.10.11.6–9). It agrees closely with examples of *M. h. continentis* from Thailand but is slightly larger in some respects (Table 6), approaching *M. h. hasseltii* from the Malay Peninsula and Java, or the specimens from Sri Lanka discussed by Hill (1976*a*). The second upper premolar (pm^3) of the Burmese specimen is very small, totally intruded from the row, with pm^2 and pm^4 in contact, while pm_3 is small, slightly intruded but nevertheless separates pm_2 and pm_4.

No examples of *M. hasseltii* were obtained by 'Operation Drake' in Sulawesi, whence its reported occurrence apparently rests on specimens recorded by Jentink (1887, 1888) from Gorontalo in the northern part of the island.

Myotis adversus moluccarum (Thomas, 1915)

Leuconoe moluccarum Thomas, 1915*d* : 170. Ara, Kei Islands.
Anamygdon solomonis Troughton, 1929 : 89. Rovianna I, New Georgia group, Solomon Is.

Specimens examined. C Sulawesi: 2 ♂♂, ♀ BM(NH) 82.131–133 R Ranu, 1° 51′ S, 121° 30′ E (in alcohol, skulls extracted; coll. B. H. Gaskell, 'Operation Drake').

Remarks. Tate (1941*d*) referred specimens of *M. adversus* from Sulawesi, Peleng Island and West Irian to *M. a. moluccarum,* with which these agree closely. They are rather smaller than *M. a. adversus* (Horsfield, 1824) from Java: the Bornean and Sumatran subspecies *M. a. carimatae* Miller, 1906*d* is very similar to *moluccarum* but only limited material is available for comparison.

Myotis adversus orientis subsp. nov.

Holotype. New Hebrides: ♀ BM(NH) 73.1412 Eastern cave at cliff base behind Aouta Plantation, Aore I. Collected 24 August 1971 by the Earl of Cranbrook, presented by the Royal Society Expedition to the New Hebrides, 1971. Original number 104–02. Skin and skull.

Other material. New Hebrides: 3 ♂♂, 7 ♀♀ BM(NH) 73.1404–1411, 73.1413 (in alcohol, skulls extracted), 73.1414 (skin, skull). All from type locality (obtained Earl of Cranbrook, Royal Society Expedition to the New Hebrides, 1971).

Diagnosis. A member of the subgenus *Leuconoe,* generally slightly larger (Table 7) in most respects than the geographically adjacent *M. a. moluccarum* from the Solomon Islands, New

Table 7 Measurements of *Myotis adversus* (number of specimens examined in parentheses).

	M. a. adversus Java	*M. a. carimatae* Borneo	*M. a. moluccarum* Sulawesi–Solomon Is	*M. a. macropus* Australia	*M. a. orientis* New Hebrides	*M. a. orientis* Holotype ♀ BM(NH) 73.1412
Length of forearm	(25) 41·7–44·0	39·8, 40·2	(27) 37·5–42·1	(8) 36·6–40·4	(11) 41·1–43·9	43·2
Greatest length of skull	(6) 17·0–17·4	16·3, 16·5	(8) 15·4–16·3	—	(10) 15·6–16·3	15·9
Condylobasal length	(6) 15·2–15·8	14·9, 15·2	(9) 14·4–15·1	—	(10) 14·8–15·5	15·0
Condylocanine length	(6) 14·4–14·9	14·0, 14·1	(9) 13·4–14·3	—	(10) 14·1–14·7	14·3
Least interorbital width	(6) 4·1–4·3	4·0, 4·1	(9) 3·8–4·2	3·9, 4·0	(10) 4·3–4·6	4·4
Zygomatic width	(3) 10·4–10·5	—, 10·4	(3) 9·9–10·2	—	(5) 9·9–10·1	10·1
Width of braincase	(6) 7·9–8·0	7·2, 7·2	(9) 7·4–8·0	—	(10) 7·8–8·3	8·0
Mastoid width	(6) 8·5–8·7	8·5, 8·6	(9) 7·9–8·5	—	(10) 8·0–8·3	8·3
c^1–c^1 (alveoli)	(6) 4·5–4·8	4·5, 4·5	(9) 4·3–4·6	(3) 4·4–4·5	(10) 4·5–4·8	4·6
m^3–m^3	(6) 6·7–7·0	6·4, 6·5	(9) 6·2–6·8	(3) 6·3–6·5	(10) 6·7–7·0	6·9
c–m^3	(6) 6·2–6·4	5·9, 6·0	(9) 5·7–6·2	(3) 5·8–6·1	(11) 5·9–6·1	6·0
Length of complete mandible from condyles	(5) 11·6–11·9	11·3, 11·5	(6) 11·1–11·3	(3) 10·9–11·3	(6) 11·2–11·6	11·4
Length of right ramus	(6) 12·1–12·5	11·6, 11·8	(9) 11·0–11·8	(3) 11·1–11·6	(10) 11·7–12·0	11·7
c–m_3	(6) 6·6–6·9	6·3, 6·3	(9) 6·1–6·5	(3) 6·2–6·5	(11) 6·4–6·5	6·4

Guinea, the Moluccas and Sulawesi, approaching *M. a. adversus* from Java in size; differing from these, from *M. a. carimatae* from Borneo and from *M. a. macropus* (Gould, 1855) from Australia in a slightly greater degree of frontal elevation of the rostrum, the frontal profile less concave, in wider, more substantial interorbital region, and in greater inflation of the braincase, which is more globose, especially anteriorly, slightly higher, and more elevated posteriorly.

DESCRIPTION. Externally very like *M. a. adversus* or *M. a. moluccarum* with relatively large, rounded ears reaching almost to tip of muzzle when laid forward; tragus in length a little less than half length of ear, slender, pointed, its anterior margin straight, its posterior margin gently convex; wing inserted at ankle. Pelage dense and woolly, dorsally blackish brown, the hairs dark at the base and for most of their length, tipped lightly with greyish or buffy white, the tipping forming no more than a slight overlay, the ventral surface greyish white, the hairs blackish at the base, heavily and densely tipped with grey white, posteriorly with little or no black at the base. Dorsal pelage darker and blacker than brownish examples of *moluccarum* from Sulawesi and the Molucca Islands but these are old specimens that have been preserved for many years: a similarly old specimen from Choiseul Island in the Solomon Islands approaches examples from the New Hebrides in dorsal colour.

Skull strongly constructed, with broad, high rostrum, its upper surface flattened posteriorly with a broad, shallow median longitudinal depression; frontal profile only slightly depressed; interorbital region broad, relatively massive, least interorbital width 28–30% of condylobasal length, 54–57% of width of braincase; 26–28% of condylobasal length, 49–54% of width of braincase in *adversus, carimatae* and *moluccarum*; braincase inflated, globose, anteriorly relatively full, elevated posteriorly; palate short and wide, with strong post-palatal spine, supported by thin lateral laminae; second upper premolar (pm^3) small, its crown area about one third crown area of anterior tooth (pm^2), almost in row, slightly intruded, or intruded from row to lie in a recess between pm^2 and last upper premolar (pm^4); second lower premolar (pm_3) in crown area about one third crown area of anterior tooth (pm_2), almost in row but compressed between pm_2 and last lower premolar (pm_4), or sometimes slightly intruded.

Measurements of *M. a. orientis* appear in Table 7.

ETYMOLOGY. An eastern representative of *M. adversus.*

DISCUSSION. Excluding very large species such as *M. macrotarsus* (Waterhouse, 1845) from the Philippine Islands and northern Borneo and *M. stalkeri* Thomas, 1910*a* from the Kei Islands leaves in Indo-Australia a group of large-footed bats of the subgenus *Leuconoe* with forearms ranging in length from 36–44 and with pm^2 and pm_3 variably reduced and variably situated in the toothrows. Their current classification has been established by views and opinions scattered through several publications. These include Tate (1941*d*), Medway (1965, 1977), Findlay (1972), Hill & Thonglongya (1972) and Hill, (1972, 1974, 1976*a*). The arrangement adopted here has been developed from these and may be summarized:

1.	Wing inserted on metatarsus	*M. horsfieldii*
	Wing inserted at end of tibia or at ankle	2
2.	Fur short, velvety; post-palatal extension short, its median spicule lacking thin bony supporting laminae; pm^3 minute, intruded, pm^2 and pm^4 in contact or nearly so, pm_3 small, only partially in row or completely intruded	*M. hasseltii*
	Fur, dense, woolly; post-palatal extension long, its median spicule supported by thin bony laminae; pm^3_3 not greatly reduced, pm^3 not usually much intruded, pm_3 usually in row or only slightly intruded	*M. adversus*

Myotis horsfieldii deignani Shamel, 1942 — Thailand, Hainan I, Hong Kong (Findley, 1972).

Myotis horsfieldii horsfieldii (Temminck, 1840) (incl. *lepidus* Thomas, 1915*d*)	Malaya, Borneo, Java, Bali, Sulawesi.
Myotis horsfieldii (?) *peshwa* Thomas, 1915*a* (see Hill, 1976*a*)	India.
Myotis horsfieldii (?) *dryas* Andersen, 1907*b* (see Hill, 1976*a*)	South Andaman I.
Myotis horsfieldii (?) *jeannei* Taylor, 1934	Zamboanga I, Philippine Is.
Myotis hasseltii continentis Shamel, 1942	Burma, Thailand, Kampuchea, (?) Sri Lanka.
Myotis hasseltii hasseltii Temminck, 1840	Malaya, Rhio Archipelago, Sumatra, Java.
Myotis hasseltii macellus Temminck, 1840	Borneo.
Myotis hasseltii (?) *abbotti* Lyon, 1916	North Pagi I, Mentawei Is, off W Sumatra.
Myotis adversus adversus Horsfield, 1824	Java, (?) Malaya.
Myotis adversus carimatae Miller, 1906*d*	Borneo, Karimata I.
Myotis adversus moluccarum Thomas, 1915*d*	Sulawesi, Molucca Is, New Guinea, Solomon Is.
Myotis adversus orientis Hill, 1983	New Hebrides.
Myotis adversus macropus Gould, 1855	Australia.

Pipistrellus javanicus (Gray, 1838)

Scotophilus javanicus Gray, 1838 : 498 (renaming of *Vespertilion javanais* F. Cuvier, 1832). Java.

SPECIMENS EXAMINED. C Sulawesi: ♀ BM(NH) 82.134 R Ranu, 1° 51′ S, 121° 30′ E (in alcohol, skull extracted; coll. B. H. Gaskell, 'Operation Drake').

REMARKS. This specimen from Sulawesi agrees in most respects with examples of *P. javanicus* from Java and from the island of Madura. It differs from these only in the slightly greater concavity of its rostral profile, in having the frontal part of the braincase a little more inflated and in a slightly higher posterior upper canine cusp. Measurements: length of forearm 32·1; greatest length of skull 13·6; condylobasal length 12·7; condylocanine length 12·3; least interorbital width 3·5; zygomatic width 8·6; width of braincase 6·7; mastoid width 7·3; c^1–c^1 (alveoli) 4·3; m^3–m^3 6·2; c–m^3 4·9; length complete mandible from condyles 9·4; length right ramus from condyle 9·8; c–m_3 5·2.

DISCUSSION. Several species of *Pipistrellus* have been reported or described from Sulawesi. These include *P. javanicus* (Gray, 1838) by Dobson (1878) (as *abramus,* a subspecies of *P. javanicus* according to Laurie & Hill, 1954), Meyer (1899) (as *abramus*) and Shamel (1940) (also as *abramus*); *P. imbricatus* (Horsfield, 1824) by Tate (1942*b*); possibly *P. papuanus* (Peters & Doria, 1881) by Laurie & Hill (1954); *P. petersi* (Meyer, 1899), described from northern Sulawesi and reported again by Shamel (1940) and Tate (1942*b*), and *P. minahassae* (Meyer, 1899), also described from northern Sulawesi and again reported provisionally by Tate (1942*b*). Of specimens recorded as *abramus* by Dobson (1878), one (BM(NH) 72.4.11.4) from northern Sulawesi is neither *javanicus* nor is it *papuanus,* as Laurie & Hill (1954) thought it might be, so far as can be judged from the damaged skull. A second specimen, a skin only, cannot be found. The cranial features of the holotypes of *petersi* and *minahassae* have never been recorded, but Tate (1942*b*) provides information and measurements drawn from the referred specimens that he reported.

There are few records of specimens referable to *P. javanicus* from the area east of Java and Sulawesi. I have examined specimens supposedly of this species in the collection of the Zoologisches Museum (Museum für Naturkunde), Berlin from Bali (ZMB 90465, 90468–90471) and from Sumba Island (ZMB 92152–92157), the latter those reported as *P. tralatitius* (=*P. javanicus*) by Pohle (1950). None in fact represent *P. javanicus* but instead are examples of *Myotis muricola,* recorded from Sumba by Forcart (1952). Schwarz (1914) reported *P. tralatitius* from Timor Island, but these records from Lelogama and Bonleo may refer to *P. tenuis* as Goodwin (1979) suggested. Other specimens from Timor recorded as *P. tralatitius* by Pohle (1950) prove (vide infra) to be examples of *P. tenuis*. Dobson (1878) recorded two specimens of *Pipistrellus abramus* from 'Australia', having earlier (1876) suggested that the species extended to that country. These are BM(NH) 47.7.21.12–13, in alcohol: their skulls have now been extracted. The two specimens agree closely with *P. javanicus* which evidently they represent: a further specimen, BM(NH) 80.1.17.4 from the Aru Islands may also represent this species but is rather smaller.

Pipistrellus tenuis papuanus (Peters & Doria, 1881)

Vesperugo papuanus Peters & Doria, 1881 : 696. Salawatti, West Irian, NW New Guinea.
Vesperugo papuanus orientalis Meyer, 1899 : 14. Bongu, Astrolabe Bay, Papua New Guinea.

Specimens examined. Papua New Guinea: ♂, ♀♀ BM(NH) 73.2046–2048 Kairiru I, near Wewak, East Sepik (in alcohol; coll. Aberdeen University Exploration Society Expedition to New Guinea, 1973); ♀♀ BM(NH) 80.644–645 Wau Gulf, Morobe, 7° 19′ S, 140° 44′ E; ♀♀ BM(NH) 80.646–651 Lae, Morobe, c. 6° 49′ S, 147° 03′ E; ♂. ♀♀ BM(NH) 82.148–152 Cave near Avi, Mt. Hagen (all in alcohol; coll. B. H. Gaskell, 'Operation Drake'); ♀ BM(NH) 82.157 Lake Murray Wildlife Station, Boboa, Western Province (in alcohol; coll. I. M. Redmond).

Remarks. These specimens with forearm lengths ranging from 29·3–31·6 are in good agreement with *P. t. papuanus* as represented in the collections of the British Museum (Natural History).

Discussion. Laurie & Hill (1954) recognised *papuanus* as a distinct species in New Guinea, together with *P. angulatus* of which they listed three subspecies, *P. a. angulatus* Peters, 1880 from the Bismarck Archipelago, *P. a. collinus* Thomas, 1920 from mainland New Guinea and *P. a. ponceleti* Troughton, 1936 from the Solomon Islands, in general following the leads provided by Tate (1942*b*). Lidicker & Ziegler (1968) adopted the classification offered by Laurie & Hill but tentatively raised *ponceleti* to specific rank, and added *P. imbricatus* (Horsfield, 1824) to the New Guinea list by referring specimens from Balim River, West Irian and Emirau Island in the Bismarck Archipelago to that species. More recently, Koopman (1973) has reviewed the Indo-Australian pipistrelles associated with *P. tenuis,* with particular reference to the forms known from New Guinea. His study led him to unite *papuanus, angulatus, collinus* and *ponceleti* (and also *nitidus* Tomes, 1858 from Borneo (referred to *P. tenuis* as a subspecies by Medway, 1965), *subulidens* Miller, 1900 from Sirhassen Island, *sewelanus* Oey, 1960 from Lombok Island and *murrayi* Andrews, 1900 from Christmas Island) into a single species, *P. tenuis* (Temminck, 1840). He mentioned but did not discuss the records of *P. imbricatus* by Lidicker & Ziegler.

Although the collections of the British Museum (Natural History) include a substantial number of specimens that can be referred to *P. t. papuanus,* there are few that can be confidently identified with *collinus, angulatus* or *ponceleti.* However, there is some evidence to confirm Koopman's (1973) division of Papuan examples into a small, relatively lowland form (*papuanus*) and a larger highland form (*collinus*), separated also by the dimensions of the palate, which is relatively short and narrow in the lowland form but longer and wider in the montane form. Additionally, montane specimens have a concave rostral profile in contrast to the flatter, less depressed profile usual in lowland examples. No montane specimens are available from West Irian, but lowland examples from the western part of the island confirm the indication by Koopman (Figs. 1, 3) that here the lowland form has a longer skull nearer in size to that of the montane form, with a correspondingly slightly longer and slightly wider palate. However, Koopman examined only three variables and it is also clear from his diagrams (Figs. 1–3) that high montane (especially above 1800 m) specimens differ considerably from those from lower altitudes in the dimensions of the palate: those from altitudes of 1000–1800 m in Papua ally themselves in palatal size with the high montane examples (Fig. 2) but in West Irian (Fig. 3) with more truly lowland specimens. Similarly, in length of skull (Fig. 1) specimens from the intermediate zone in Papua are like those from higher altitudes but in West Irian are approached in size by lowland examples. The variation in eastern New Guinea and its associated islands has been analysed in greater detail by Koopman (1982). *Pipistrellus tenuis papuanus* also occurs on the Bismarck Archipelago whence Smith & Hood (1981) have recorded specimens that they refer to this form, together with other larger examples that apparently represent *angulatus*, the two perhaps being separated also by roosting preference. Moreover, specimens examined by Koopman (1973) from New Britain with forearms 28–30 in length may also represent *P. t. papuanus.*

It is unlikely that specimens from Emirau Island, Bismarck Archipelago and from the Balim River, West Irian represent *P. imbricatus* as Lidicker & Ziegler (1968) averred. According to these authors the specimen from Emirau (from their illustration, fig. 4) has a concave rostral profile and has an anterior upper premolar (pm^2) of cross-sectional area about equal to two thirds of the cross-sectional area of the outer upper incisor (i^3). However, in a series of *P. imbricatus* from Java in the British Museum (Natural History) the rostral profile is straight or nearly so, a point reinforced by Koopman (1973) who recorded that *imbricatus* has a flat, not concave forehead, and pm^2 is very small, sometimes minute, not more and usually less than one third the cross-sectional area of i^3. Tate (1942) identified the Balim River specimens (AMNH 109979–109980) as *'P. imbricatus collinus'*, and Smith & Hood (1981) suggest that for the present the Emirau specimen seems best referred to *angulatus.*

Pohle (1950) recorded *P. tralatitius* (=*P. javanicus*) from Timor on the basis of specimens in the Zoologische Museum (Museum für Naturkunde), Berlin, collected by G. Stein in 1932. I have examined the skulls of these specimens (ZMB 92107–92111), all from Tjamplong and they prove not to represent *P. javanicus* but to be closely similar to if not identical with *P. tenuis papuanus.* Goodwin (1979) also reports *P. tenuis* from Timor, and gives measurements (taken by Dr K. F. Koopman) of further specimens from Tjamplong collected by Stein and now in the Museum Zoologicum Bogoriense, Bogor. Two specimens reported from Timor by Schwarz (1914) as *P. tralatitius* may also be *P. tenuis*, as Goodwin suggests. Koopman (1973) allocates Timorese specimens to *P. t. sewelanus,* along with those from Sulawesi.

Collett (1897) recorded a single specimen from Roebuck Bay, near Broome, northwestern Australia as *P. tenuis.* This specimen, collected by Dahl and now in the Oslo Museum, was sent to the British Museum (Natural History) in 1966 for examination. It proved to agree closely with *P. t. papuanus* but to be slightly larger cranially, with a narrower, blade-like post-palatal spine and slightly less prominent basioccipital pits, and to have a slightly less prominent posterior upper canine cusp. More recently, in 1976, two specimens (AMNH 216135–216136) from the collections of the American Museum of Natural History were examined for Dr Karl F. Koopman. These agree basically with *P. t. papuanus* but have the narial emargination a little more rounded and less acute posteriorly, the palate slightly more domed and less prominent posterior cusps on the upper canines. Although for the present I would refer these specimens to *P. t. papuanus* it seems probable that more material might well show the Australian population to be subspecifically separable.

The limited material in the British Museum (Natural History) supports the association of *papuanus* with *tenuis* as Koopman (1973) proposed, although of the latter only two so-called 'cotypes' (BM(NH) 7.1.1.407–408) are available for the study, Tate (1942*b*) having selected as lectotype a specimen in the Rijksmuseum van Natuurlijke Historie, Leiden. On the basis of this sample I am inclined to agree that *tenuis* and *papuanus* are conspecific: both are characterised by small size, short premaxillae, the narial emargination quite sharply narrowed posteriorly, the anterior upper premolar (pm^2) moderate in size, situated in the internal angle between c^1 and the posterior upper premolar (pm^4), which almost touch or are in contact. Of the two forms, *P. t. tenuis* is apparently slightly the larger: it is similar in size to a small series of *murrayi* from Christmas Island which also clearly represents *P. tenuis* and may even be synonymous with the nominate subspecies. A specimen (AMNH 107827) in the American Museum of Natural History from Bratan, Bali examined in 1970 for Dr Karl F. Koopman also represents this complex. Then labelled *'Pipistrellus (coromandra) imbricatus* subsp' which very evidently it is not, it is apparently the example identified by Tate (1942*b*) as *P. tenuis.* It is similar to the 'cotypes' of *tenuis* or to *murrayi* but the skull is a trifle longer and wider and the toothrows slightly longer, in these respects approaching *papuanus.* Koopman (1973) refers specimens from Bali and Java to *P. t. nitidus.* The cranial measurements of specimens discussed appear in Table 8.

Pipistrellus vordermanni (Jentink, 1890)

Vesperugo vordermanni Jentink, 1890 : 152. Billiton I.

SPECIMEN EXAMINED. Borneo: ♀ BM(NH) 82.547 Samunsan Wildlife Sanctuary, Sarawak. (in alcohol, skull extracted; coll. N. A. MacKenzie).

REMARKS. This is the first of *P. vordermanni* to be recorded from Borneo; no direct comparison has been possible but the specimen agrees closely with the original account by Jentink. Among Bornean pipistrelles the species may be readily recognised by its large ears, slightly hatchet-shaped tragus with anteriorly directed point, whitish wings, short skull, full, rounded braincase and short rostrum, small supraorbital tubercles, deep zygomata with distinct postorbital process, deep basial pits, minute anterior upper premolar (pm^2) which is completely intruded into a recess between the canine and the posterior upper premolar (pm^4), the two latter teeth in contact, and much reduced anterior lower premolar (pm$_2$).

DISCUSSION. Chasen (1940) synonymised *vordermanni* and *curtatus* Miller, 1911 from Engano Island, off the west coast of Sumatra, with the Sumatran *macrotis* (Temminck, 1840) which he considered a subspecies of *P. imbricatus* (Horsfield, 1824) from Java. However, all differ sharply from *imbricatus* in a decidedly shorter rostrum and consequently shorter palate, a point emphasised by Miller in his description of *curtatus.* Tate (1942*b*) treated *macrotis, vordermanni* and *curtatus* as distinct species, associating them with *P. cadornae* Thomas, 1916 from Burma in the *savii* group of *Pipistrellus.* Hill (1962) followed Tate in considering *macrotis* and *vordermanni* distinct species but removed them, with *cadornae,* from any close relationship with *P. savii* (Bonaparte, 1837). As Tate (1942*b*) pointed out, the four forms clearly constitute an assemblage characterised by the cranial and dental characters noted above. The larger size of *cadornae* sets it rather apart from *macrotis, vordermanni* and *curtatus* which may well prove to be conspecific.

Measurements of the Bornean example of *vordermanni* with (in parentheses) those of an example (BM(NH) 23.1.2.12) of *macrotis* from Sebang, Sumatra: length of forearm 30·5 (31·5); length of ear 15·1 (14·7); greatest length of skull 11·4 (12·2); condylobasal length 11·1 (11·8); condylocanine length 10·8 (11·5); width across supraorbital tubercles 4·6 (4·7); zygomatic width 8·2 (8·4); least interorbital width 3·5 (3·5); width of braincase 6·4 (6·5); mastoid width 7·0 (7·3); c^1–c^1 (alveoli) 4·0 (3·9); m^3–m^3 5·1 (5·3); c–m^3 3·8 (4·0); length of complete mandible from condyles — (7·8); length of right ramus from condyle — (8·3); c–m$_3$ 4·2 (4·4). Measurements of type material of *macrotis, vordermanni* and *cadornae* are given by Tate (1942*b*) and of the holotype and additional specimens of *cadornae* by Hill (1962).

Table 8 Selected cranial measurements of *Pipistrellus tenuis* (number of specimens examined in parentheses).

	P. t. tenuis Sumatra 'Cotypes'	Bali	*P. t. murrayi* Christmas I	Timor	*P. t. papuanus* New Guinea	Australia
Condylocanine length	—	11·3	(6) 10·8–11·0	(3) 10·8–11·0	(14) 10·2–11·6	(3) 10·3–11·0
Width of braincase	—	6·2	(6) 5·9–6·3	(5) 5·8–6·1	(13) 6·0–6·6	(3) 6·0–6·3
Mastoid width	—	6·8	(6) 6·6–6·8	6·7, 6·8	(14) 6·6–7·3	(3) 6·9–7·1
c^1–c^1 (alveoli)	—, 3·5	3·7	(6) 3·4–3·9	(5) 3·8–4·1	(15) 3·6–4·2	(3) 3·5–4·2
m^3–m^3	—, 4·8	5·2	(6) 4·8–5·1	(5) 5·2–5·6	(15) 5·0–5·7	(3) 4·8–5·6
c–m^3	3·5, 3·7	4·4	(6) 4·0–4·2	(5) 4·1–4·4	(15) 3·8–4·4	(3) 3·8–4·3

Pipistrellus societatis Hill, 1972

Pipistrellus societatis Hill, 1972 : 34. Base Camp, Gunong Benom, Pahang, Malaya, 800 ft, 3° 51′ N, 102° 11′ E.

SPECIMEN EXAMINED. Malaya: ♀ BM(NH) 81.1802 Sungai Tekam Forest Reserve, Pahang (in alcohol, skull extracted; coll. A. O. Johns).

REMARKS. This is the first example of *P. societatis* to be reported since its description, the holotype (BM(NH) 67.1605) being then the only known example. This newly obtained specimen is in good general agreement with the holotype but is slightly larger in some respects and has, however, a small, low sagittal crest that is absent from the original example. The narial emargination is very slightly narrowed posteriorly and the last upper molar (m^3) is slightly less reduced than in the holotype, with a more evident but small metacone and short third commissure, although as in the holotype the tooth is flattened antero-posteriorly and more platelet-like when compared with the closely related species *P. circumdatus*. As in the holotype the hypoconid and entoconid of the last lower molar (m_3) are also slightly reduced in comparison with those of the related species.

Measurements: length of forearm 39·4; greatest length of skull 15·0; condylobasal length 14·3; condylocanine length 14·1; length orbit–gnathion 3·9; palatal length, excluding post-palatal spine 6·7; length palatal bridge, excluding post-palatal spine 5·1; width across ante-orbital foramina 3·2; lachrymal width 6·8; width across supraorbital tubercles 6·0; zygomatic width 10·5; least interorbital width 4·3; width of braincase 7·5; mastoid width 8·4; c^1–c^1 (alveoli) 4·8; m^3–m^3 7·0; c–m^3 5·5; length of complete mandible from condyles 10·6; length of right ramus from condyle 11·0; c–m_3 5·9.

DISCUSSION. Hill (1972, 1974) reported an example of the closely related *P. circumdatus* from Fraser's Hill, Pahang. Certain features of this species and of *P. societatis* tend towards the Australian genus *Chalinolobus* and more distantly towards the nominal genus *Glauconycteris* from Africa. Both species show an approach to *Chalinolobus* in the development of a slightly pendent lobule at the base of the outer margin of the ear, inserted a little behind and below the angle of the mouth, in an elevated, rounded braincase and the inflation of the supraorbital region, a shortening of the rostrum and a narrowing of the anterior palatal emargination, the arrangement of the upper incisors into a straight line and the reduction of the anterior upper premolar (pm^2) almost to the point of obsolescence.

Philetor brachypterus rohui Thomas, 1902

Philetor rohui Thomas, 1902 : 220. Albert Edward Range, eastern Papua New Guinea, 6000 ft.

SPECIMENS EXAMINED. Papua New Guinea: ♂, ♀♀BM(NH) 80.652–656, ♂ BM(NH) 80.694 Buso, Morobe, 6° 41′ S, 147° 13′ E (in alcohol; coll. B. H. Gaskell; 'Operation Drake').

Philetor brachypterus verecundus (Chasen, 1940)

Eptesicus verecundus Chasen, 1940 : 53. Mt. Kledang, Perak, Malaya, 2646 ft.

SPECIMEN EXAMINED. Borneo: ♂ BM(NH) 78.1542 Gunung Mulu, Sarawak, 2600 ft (in alcohol; coll. D. R. Wells, Royal Geographical Society Expedition to Gunung Mulu, 1977–78).

REMARKS. This species has been recorded previously from two Bornean localities, Pangkalan Lobang, at Niah, Sarawak, and Poring National Park, at Ranau in Sabah (Lim, Chai & Muul, 1974; Medway, 1977). Two of these specimens were examined at the British Museum (Natural History) in 1975 and found to approach *P. b. rohui* from New Guinea in the width of the narial emargination rather than *P. b. verecundus* from Malaya. However, a specimen (BM(NH) 73.597) from Ulu Gombok, Selangor, Malaya has a similarly narrower emargination and as Medway (1977) suggests, this feature seems of little value in establishing subspecies. Among specimens in the British Museum (Natural History) the forearm of those of *P. b. verecundus* is a little longer on the whole than in *P. b. rohui*: in twenty Malayan examples the length of the forearm ranges from 33·0–37·6, in thirty one from New Guinea from 31·3–35·6. In size the Bornean example (length of forearm 35·4) agrees with those from Malaya (Lim, Chai & Muul, 1974, give forearm lengths of 33–36 for eight further specimens from Borneo). However, Kock (1981) records specimens from New Britain in the Bismarck Archipelago and from New Guinea that are similar in forearm length to those from Malaya. For the present Bornean specimens are referred to *P. b. verecundus*, but subspecific validities are very provisional in *P. brachypterus*, the features of its Sumatran representative, (nominally *P. b. brachypterus*) remaining largely unknown (Hill, 1966*b* 1971*b*). The collections in London include an unreported series (BM(NH) 74.415–434) of *P. b. verecundus* from Paloh Forest Reserve, Paloh, Kluang, Johore, Malaya.

Hesperoptenus (Milithronycteris) gaskelli sp. nov.

HOLOTYPE. Central Sulawesi: ♀ (yg. ad.) BM(NH) 82.135. River Ranu, 1° 51′ S, 121° 30′ E. Collected 19 April 1980 by B. H. Gaskell, 'Operation Drake'. In alcohol, skull extracted.

DIAGNOSIS. Characteristically a member of the subgenus *Milithronycteris* similar in many respects to *H. tickelli* or *H. tomesi*, differing principally from *H. blanfordi* in much larger size, naked internarial region, the dorsal surface of the forearm lacking any dense covering of hair, the absence of a fleshy pad at the base of the thumb, inflated braincase, narrow post-orbital region and relatively less reduced outer upper incisors (i^{3-3}) and last upper molars (p^{3}_{3}). Differing from *H. tickelli* and *H. tomesi* in smaller size and smaller teeth (a comparison of the young adult holotype with two examples of *H. tickelli* of similar or even slightly younger age shows the dentition of the latter to be substantially larger) the canine and post-canine teeth little more than one half the basal area of their counterparts in *H. tickelli*, and for the most part rather less than one half the basal area of those of *H. tomesi*, inner upper incisors (i^{2-2}) similarly smaller, the lower incisors about one third smaller than those of *H. tickelli* and about half the size of those of *H. tomesi*. Differing further from *H. tickelli* in its rich, dark, blackish rather than yellowish brown or straw brown overall coloration, in much shortened second phalanx of the third digit, in the development of small supraorbital tubercles and slightly more vertical orbital margin, deeper, more sharply sculpted basioccipital pits, a narrower cingulum on the outer upper incisor (i^3), more flattened last upper molar (m^3) and a slightly greater degree of reduction of the last lower molar (m_3); from *H. tomesi* in a lesser degree of intrusion of the outer upper incisor (i^3), in a lack of thickening of the first and second lower incisors (i_{1-2}) and a less thickened outer lower incisor (i_3), its cusp pattern remaining evident.

DESCRIPTION. Muzzle low, wide, laterally swollen, sparsely pilose, with medianly a very shallow longitudinal groove behind the nostrils; narial openings nearly circular, moderately separated; a few sparse, short hairs fringing the upper lip beneath nostrils, the hairs laterally longer and rather denser; internarial region nearly naked; upper part of muzzle anteriorly with a sparse cover of long hairs, a short, broad median longitudinal band of similar hairs extending from a point about halfway between nostrils and eyes to widen posteriorly between ears and join fur of crown; lateral parts of upper lip above canines and premolars swollen, sparsely furred, the hairs usually stiff and bristle-like; sides of muzzle around and beneath eyes nearly to angle of mouth with a thin cover of longer hairs; a small wart above the anterior canthus of the eye, bearing a long vibrissa and a few shorter hairs; lower lip with a small, undivided median pad; anteriorly ventral surface of head only sparsely pilose with a small almost totally naked area beneath the symphysis menti, preceding a low, almost imperceptible elevation that bears a few long hairs; a few longer vibrissae at sides of muzzle.

Ear thick and fleshy, subquadrangular, its anterior margin with well developed posteriorly directed lobe at its base, proximally strongly convex, distally almost straight, the tip broadly rounded, posterior margin of ear strongly convex, with prominent fleshy antitragal lobe, the lobe thickened along its outer margin, inserted quadrately behind and a little below the angle of the mouth; tragus rather fleshy, slightly less in length than one half the length of the ear, more or less hatchet shaped, its anterior margin straight to a narrow, more or less anteriorly directed tip, its upper margin horizontal, the posterior margin strongly convex to well developed subtriangular basal lobe; outer surface of conch quite densely haired in its basal half, distal parts of inner surface and lower part of outer face of tragus sparsely haired.

Thumb relatively long; third metacarpal slightly the longest of metacarpals two to five, fourth very little shorter, fifth rather more so, the second the shortest; second phalange of third digit shorter than first phalange; upper surface of thumb with a thin cover of short hairs; upper surface of forearm naked except for a few hairs near the elbow; toes sparsely haired dorsally; upper surface of uropatagium sparsely haired for its proximal half; base of tail similarly furred both above and below, its tip protruding beyond uropatagium; calcar long, extending across about two thirds of the uropatagial margin; a small linear post-calcarial lobe, lacking any definite supporting cartilaginous spur.

Colour (from specimen in alcohol) both above and below a rich dark blackish chocolate brown, the hairs more brownish at the base but otherwise darker and lustrous.

Skull evidently of medium size with broad, uninflated braincase; postorbital region moderately constricted; supraorbital region abruptly expanded, with well developed superior anteorbital tubercles; anterior orbital margin sharply defined, in frontal aspect nearly vertical; anteorbital foramen large, closed by a narrow bar of bone; maxillary margin of orbit heavy, flange-like, in ventral view forming a wide ledge alongside the toothrow; zygomata slender; narial emargination more or less U-shaped, slightly tapered posteriorly, with broadly rounded apex; post-palatal extension short, with broad median spine; basioccipital pits prominent, sharply incised into basioccipital.

Inner upper incisor (i^2) caniniform, massive, unicuspid, at its base equal in area almost to one half the basal area of the canine, with well developed cingulum, anterior face of tooth rounded, its postero-internal face deeply excavated, its postero-external face shallowly so, the depressions separated by a narrow ridge; outer upper incisor (i^3) more or less ovate, with wide basin-like cingulum and central three-faced cusp, basal area of tooth a little less than one half basal area of i^2, the cusp extending a little above the cingula of i^2 or of c^1, its postero-internal face excavated; tooth intruded from row to lie almost directly behind i^2, its anterior edge in contact with that tooth and on a line joining the anterior edges of c^{1-1}, its posterior edge on a line joining the centres of these teeth, its labial part intruded between i^2 and c^1, with its postero-lateral edge in contact with the antero-lateral face of c^1; i^2 and c^1 otherwise separated by a narrow interspace of about one third the basal diameter of i^2. Upper canine with strong cingulum; upper premolar (pm^4) slightly compressed in toothrow; last upper molar (m^3) in crown area about one half crown area of m^1, with metacone and three commissures, the third short. Lower incisors (i_{1-3}) with tricuspid cutting edge, i_2 overlapping i_1 by almost one half its width, i_3 thickened, with low, small posterior supporting cusp, similarly imbricating i_2; anterior lower premolar (pm_2) in crown area about one third crown area of posterior lower premolar (pm_4), slightly compressed in row; last lower molar (m_3) little reduced, entoconid and hypoconid low, the tooth slightly narrowed posteriorly.

MEASUREMENTS. External measurements of holotype with (in parentheses) those of two males (BM(NH) 13.2.10.27–28) of *H. tickelli* from Sri Lanka, of similar or younger age: length of forearm 40·1 (47·9, 48·2); of thumb with claw 6·0 (7·9, 8·3); of II^m 35·3 (38·9, 41·3); of III^m 36·3 (41·4, 43·3); of III^1 16·2 (17·5, 19·0); of III^2 13·3 (16·1, 16·6); of IV^m 36·0 (40·8, 41·6); of IV^1 13·4 (14·6, 16·1); of IV^2 7·8 (9·6, 10·7); of V^m 35·1 (39·8, 41·1); of V^1 8·4 (10·1, 10·4); V^2 4·9 (7·8, 7·7); length of tibia 16·5 (19·1, 20·4).

Cranial measurements of holotype with (in parentheses) those of BM(NH) 13.2.10.27: greatest length of skull 15·6 (17·1); condylobasal length 15·2 (—); condylocanine length 13·1 (—); length orbit–gnathion 4·0 (4·7); palatal length 5·9 (7·0); width across anteorbital foramina 5·6 (6·3); width across front of orbits 7·8 (8·4); width across supraorbital swellings 6·6 (6·9); least interorbital width 4·7 (4·7); zygomatic width 11·4 (—); width of braincase 8·3 (9·2); height of braincase 5·8 (6·1); mastoid width 9·0 (9·8); c^1–c^1 (alveoli) 5·4 (6·1); m^3–m^3 7·8 (8·6); c–m^3 6·0 (7·0); length complete mandible from condyles 11·5 (13·0); length right ramus from condyle 12·0 (13·6); c–m_3 6·5 (7·8).

Discussion. The genus *Hesperoptenus* was reviewed in detail by Hill (1976*b*): it has not been recorded previously from Sulawesi. The nominate subgenus with the sole species *H. doriae* Peters, 1869 is known from Malaya and Borneo. In the subgenus *Milithronycteris* the small, very distinctive *H. blanfordi* (Dobson, 1877*b*) has been reported from southern Burma, Thailand and Malaya, *H. tickelli* (Blyth, 1851) from India and Sri Lanka east to the Andaman Islands and Thailand, and *H. tomesi* Thomas, 1905 from Malaya and Borneo. In coloration, shortening of the second phalanx of the third digit, the presence of well-developed supraorbital tubercles, more nearly vertical anteorbital margin, a narrow cingulum on the outer upper incisor (i^3) and in the slightly greater degree of reduction of the last upper molar (m^3) this new species approaches *H. tomesi,* although clearly very much smaller. However, its lower incisors (i_{1-3}) are relatively less massive than in *tomesi,* i_3 in particular although large and with a low posterior cingulum cusp nevertheless retaining a more obvious tricuspid edge. In these respects the new species tends towards *H. tickelli.*

Etymology. It gives me much pleasure to associate this new species with Mr B. H. Gaskell, the collector whose work with 'Operation Drake' has produced an excellent sample of the Sulawesian bat fauna.

MINIOPTERINAE

Miniopterus australis australis Tomes, 1858

Miniopterus australis Tomes, 1858 : 125. Loyalty Islands, South Pacific.

Specimens examined. New Hebrides: 2♂♂, 2 ♀♀ BM(NH) 73.1415–1418 Grotte Montmartre, near Port Vila, Efate I, 20 m; 8 ♂♂, 7 ♀♀ BM(NH) 73.1419–1433 Mission Montmartre, near Port Vila, 40 m; 5 ♂♂, 3 ♀♀ 2 undet. BM(NH) 73.1434–1443 Montmartre, near Port Vila; ♂ BM(NH) 73.1444 'Pig Cave', Narabut Camp, Efate I; 7 ♂♂, 4 ♀♀ BM(NH) 73.1445–1455 'Pig Cave', Harris Plantation, N coast of Efate I; 2 ♂♂, ♀ BM(NH) 73.1456–1458 Ijiptho Cave, NW Aneityum I, sea level; ♀, 2 ♂♂ BM(NH) 73.1459–1461 Paul's Bungalow site, near 'Bethel', Tanna I, sea level; 3 ♀♀ BM(NH) 73.1462–1464 Siwi, Tanna I; 3♂♂BM(NH) 73.1465–1467 Senwar Cave, Tenmial, NW coast of Malekula I, 40 m; ♂♂ BM(NH) 73.1468–1473 Amok, Malekula I, 485 m; 2 ♂♂, 2 ♀♀ BM(NH) 73.1474–1477 Abounatori Village, Malo I; 2 ♂♂, 4 ♀♀ BM(NH) 73.1478–1483 Aouta Plantation, Aore I; 5 ♂♂, 4 ♀♀ BM(NH) 73.1484–1492 Hog Harbour, Espiritu Santo I; ♀ BM(NH) 73.1493 Nokowoula, Espiritu Santo I; 2 ♂♂ BM(NH) 73.1494–1495 Rock shelter 'Wonatsuri', near Nokowoula, Espiritu Santo I, 3550 ft; 3 ♂♂, 3 ♀♀ BM(NH) 73.1496–1501 New Hebrides (all in alcohol except BM(NH) 73.1462, skin and skull; obtained Earl of Cranbrook, Royal Society Expedition to New Hebrides, 1971).

Type material and type locality. Tomes (1858) based *Miniopterus australis* on a total of six specimens, all apparently now in the collections of the British Museum (Natural History). The species was said originally to be from Australia but Dobson (1876) indicated that the specimens that he considered to be the 'types' came in fact from the Loyalty Islands, their bottle in the British Museum being so labelled. Later (1878) he listed these specimens as the 'types', again recording them from the Loyalty Islands. Revilliod (1914) drew attention to this contradiction and noted that Oldfield Thomas had confirmed that this latter locality was the provenance indicated on the labels of these specimens and in the relevant accession register of the British Museum (Natural History). As a result Revilliod accepted the Loyalty Islands as the correct type locality. Peterson (1981*a*) in an abstract of a paper entitled 'The systematic status of *Miniopterus australis* and related forms stated that the 'holotype' of *M. australis* supposedly from the Loyalty Islands proves to differ from population samples from these islands and from New Caledonia but is indistinguishable from the holotype of *M. tibialis* (Tomes, 1858) from Amboina in the Molucca Islands. He proposed therefore to fix the type locality of *M. australis* as eastern Australia.

Five of Tomes' original specimens were accessed by John Edward Gray, then responsible for vertebrates at the British Museum, within the registration group BM(NH) 54.5.19.1–22, a mixed collection listed without locality or ascribed variously either to the Loyalty Islands or to New Zealand, presented by Sir George Grey. Of these, BM(NH) 54.5.19.1 is recorded simply as *'Vespertilio'* without locality or further data, BM(NH) 54.5.19.4–7 being listed again as *'Vespertilio'* but with the additional data 'In spirit' and 'Loyalty Islands'. The specimen BM(NH) 54.5.19.1 is a skin with skull in situ, and has been labelled 'Australia' by J. E. Gray. Tomes' sixth specimen appears to be BM(NH) 7.1.1.555 (i.e. the Tomes collection, accessed in 1907), a skin with rostral fragment and mandible attached and according to Tomes (1858) specimen 'a' of Gray's (1843*b*) listing of *Trilatitus blepotis* from Timor, a specimen received from the Leyden Museum. Its label bears the notes 'F^{m}. B.M. Apr. 1857' and 'Timor, from the Ley. Mus.', apparently in Tomes' own hand. Evidently it was given to Tomes from the British Museum collections and was returned fifty years later when the whole of his collection was received into the National Museum.

No holotype was designated by Tomes for *M. australis* but Dobson (1876, 1878) clearly considered only the specimens in alcohol BM(NH) 54.5.19.4–7 to be the 'types'. Oldfield Thomas evidently considered this question in some detail, no doubt in response to the point raised by Revilliod, and has clearly re-bottled and in two cases labelled these specimens with appropriate annotations. The specimen tabulated as No. 1 by Tomes he considered to be BM(NH) 54.5.19.4, having labelled it 'No. 1 of Tomes'. It bears another label on which the words *'Miniopterus',* 'Loyalty Islands' and 'Sir G. Grey' in a second hand can just be discerned: a further label is no longer decipherable. This specimen is now in an individual bottle. Its external label has been written by Thomas and is annotated 'No. 1 of Tome's *australis* (No. 2 made lectotype)'. He has also written the label attached to its skull which is annotated 'No. 1 of Tome's *M. australis.* Not typical. No. 2. made lectotype'. The specimen is in fact an example of *M. robustior* Revilliod, 1914, a point made evident by Revilliod in the original account. This taxon is known so far only from the Loyalty Islands.

The remaining three alcoholic specimens are now together in one bottle with a modern external label giving their locality as Loyalty Islands. One, a male, has been labelled by Thomas as BM(NH) 54.5.19.5, the label annotated 'No. 2 of Tomes'. It is the only one of the three to have its skull extracted: the skull label has been written by Thomas and is annotated 'Lectotype'. *australis.* No. 2 of Tomes'. The other two specimens, a female and male, have no labels but are apparently 3 and 4 of Tomes. This author noted that the four specimens so far discussed were preserved in spirit in the British Museum: his 5 'a specimen in skin in the same collection, the whole of them having been collected in Australia by Sir G. Grey, K.C.B., and presented to the National Collection' is clearly BM(NH) 54.5.19.1. Its label locality, not confirmed by the accessions register, of 'Australia' may well have led Tomes to assume that all of the specimens came from that continent, whence Grey collected numerous mammals. Tomes specimen 6 is apparently BM(NH) 7.1.1.555.

Tate (1941*e*) quotes BM(NH) 54.5.19.5 as the type specimen of *M. australis,* evidently accepting the unpublished designation made by Thomas. There seems no reason either to query the validity of this selection or to doubt that the specimen is from the Loyalty Islands: it is recorded with this provenance in the accessions register and the bottle that contained it and the other three alcoholic examples registered at the same time was apparently labelled as such (Dobson, 1876, 1878) by J. E. Gray: moreover, one of these proves subsequently to belong to a taxon so far known only from these islands. Since no formal selection appears to have been made, BM(NH) 54.5.19.5 is here designated the lectotype of *Miniopterus australis* Tomes, 1858 with the Loyalty Islands as its type locality, in agreement with the archival evidence.

Maeda (1982) has provided an erroneous corollary. This author stated (p. 4) that BM(NH) 14.5.23.2 is one of Tomes' series of specimens and was re-described by Revilliod (1914) as *Miniopterus australis robustior,* remarking later (p. 7) that it is the holotype of this taxon. Both of these statements are incorrect. BM(NH) 14.5.23.2 was presented to the British Museum (Natural History) by F. Sarasin and J. Roux in 1914 and is one of the syntypes of *M. robustior*: it has no connection at all with Tomes. Revilliod (1914) makes it clear that *robustior* was based on nine examples from Lifou, Loyalty Islands and that Tomes No. 1 (now BM(NH) 54.5.19.4) must be referred to it, an allocation confirmed according to Revilliod by a cranial comparison made by Oldfield Thomas.

REMARKS. The ears of *M. australis* are rounded and lack any definite point; the tragus is more or less parallel-sided for most of its length, its upper part curving forward to a greater or lesser extent, the upper part of the anterior margin concave and the posterior part convex. The anterior projection of the upper part of the tragus is more marked in specimens from the Loyalty Islands, New Caledonia and the New Hebrides than is usual in those from more westerly localities: in the eastern specimens the tragus has a nearly horizontal upper margin, often slightly dentate, points to which Revilliod (1914) first drew attention.

The braincase is small, slightly globose but not markedly inflated, rather low, with low lambdoidal and sagittal crests, the occipital region not inflated, in profile lower than the highest point of the braincase in the frontal region; the rostrum is low, relatively wide and long, with a moderate median longitudinal sulcus; palate long, domed; there are shallow basioccipital pits, not extending anteriorly to any great extent. The upper canines are strong, with massive base and stout shaft; anterior upper premolar (pm^2) large, triangular in section, slightly compressed in row; lingual margins of m^1 and m^2 about equal, m^1 with well developed hypocone, in m^2 the hypocone evident but slightly less developed; mandibular dentition with no especial peculiarities; lower premolars (pm_{2-4}) slightly compressed.

Externally *M. australis,* if *paululus* Hollister, 1913 from the Philippines and *shortridgei* Laurie & Hill, 1957 from Java are included, is the smallest of Australasian *Miniopterus* with the length of the forearm ranging from 34·4–41·5 and of the tibia from 13·5–17·0; the tail is also relatively short, generally about 40 in length but varying from 35–45, only rarely achieving these extremes. Size differences among specimens in the collections of the British Museum (Natural History) are summarised in Table 9.

DISCUSSION. Although until recently (Maeda, 1982) thought to extend to Thailand (Lekagul & McNeely, 1977) specimens from that country in the British Museum (Natural History) represent *M. pusillus* Dobson, 1876 (then considered a subspecies of *M. australis*), as do others from the Nicobar Islands. It appears therefore that *M. australis* as understood here is distributed from the Philippine Islands, Borneo and Java east to Australia, New Caledonia and the Loyalty Islands.

Specimens from the islands of Malaita, Guadalcanal and San Christobal in the Solomon Islands have slightly longer forearms and are sometimes larger cranially than are those from the Loyalty Islands, New Caledonia and the New Hebrides. There is also a slight difference in tragal structure as already mentioned. These points in part have led Maeda (1982) to describe the Malaita and San Christobal examples as a new species, *M. solomonensis.* Specific rank seems scarcely justified for these specimens which are approached in several respects by those from some of the surrounding populations but certainly a distinct subspecies may be recognised. It is also likely that specimens from Queensland, New Guinea, the Aru Islands, Batchian Island and the Moluccan Islands of Amboina and Ceram should be separated as *M. a. tibialis* (Tomes, 1858) (considered a synonym of *M. a. australis* by Laurie & Hill, 1954) but sample sizes are small in some cases and may be misleading in the determination of subspecific limits. In Borneo *M. a. witkampi* Sody, 1930 differs little from these in contrast to the markedly smaller forms *M. a. paululus* Hollister, 1913 from the Philippine Islands and *M. a. shortridgei* Laurie & Hill, 1957 from Java. Sanborn (1952) synonymised *paululus* with *australis* with which he suggested that *tibialis* might also be synonymous. On the other hand, Peterson (1981*a*) has implied that *paululus* and *shortridgei*

Table 9 Measurements of *Miniopterus australis* (number of specimens examined in parentheses).

	Length of forearm	Condylobasal length	Width of braincase	Mastoid width	m^3–m^3	c–m^3
Philippine Is (*paululus*)	(6) 34·8–36·4	(1) 12·5	(1) 6·6	(1) 7·3	(1) 5·3	(1) 4·9
Java (*shortridgei*)	(31) 34·4–36·6	(20) 12·1–12·6	(23) 6·4–7·0	(23) 6·9–7·1	(23) 5·1–5·4	(23) 4·7–4·9
Timor (? *shortridgei*) (ex Goodwin, 1979)	(5) 35·4–38·0	(5) 12·5–12·8		(5) 7·0–7·5	(5) 5·2–5·3	(5) 4·8–5·1
Borneo (*witkampi*)	(23) 35·2–38·9	(5) 13·5–14·0	(5) 7·1–7·3	(5) 7·5–7·8	(6) 5·7–6·0	(6) 5·3–5·6
Sulawesi (*tibialis*)	(2) 37·4–40·0	(1) 13·0	(1) 6·9	(1) 7·3	(1) 5·7	(1) 5·3
Amboina (*tibialis*)	(10) 36·6–38·9	(2) 13·4–13·5	(2) 7·1–7·3	(2) 7·4–7·7	(3) 5·7–5·9	(4) 5·3–5·5
Ceram (*tibialis*)	(2) 37·2–38·4	(1) 13·2	(1) 6·9	(1) 7·3	(1) 5·7	(1) 5·3
Batchian I (? *tibialis*)	(2) 39·0–39·3	—	—	—	—	(1) 5·7
Aru Is (? *tibialis*)	(14) 37·7–41·3	(3) 13·0–13·4	(4) 7·0–7·2	(4) 7·3–7·5	(3) 5·6–5·8	(3) 5·1–5·3
Beu I, Mayabit Bay, Waigeo, West Irian (? *tibialis*)	(1) 39·3	—	—	—	—	—
Papua (ex McKean, 1972) (? *tibialis*)	(61) 37·9–40·9	(3) 12·9–13·5	(5) 6·8–7·1	—	—	(5) 5·0–5·4
Yule I, Papua (? *tibialis*)	(4) 39·7–40·8	(2) 13·7	(2) 7·2–7·4	(2) 7·8–7·9	(2) 5·8	(2) 5·5
Queensland, Australia (? *tibialis*)	(14) 37·7–39·8	(7) 13·1–13·3	(8) 6·9–7·2	(8) 7·5–7·8	(9) 5·5–5·6	(8) 5·1–5·3
San Christobal I, Malaita I, Guadalcanal I, Solomon Is (? *solomonensis*)	(15) 38·6–41·4	(8) 13·7–14·3	(8) 7·0–7·2	(8) 7·5–7·8	(11) 5·5–6·2	(10) 5·1–5·7
Rennell I (*australis*)	(26) 34·5–37·5	(7) 12·4–12·8	(9) 6·4–6·8	(9) 7·0–7·4	(9) 5·1–5·4	(10) 4·8–5·0
New Hebrides (*australis*)	(147) 34·9–38·9	(8) 12·9–13·3	(9) 6·7–7·0	(8) 7·2–7·5	(7) 5·5–5·7	(10) 5·1–5·3
Loyalty Is, New Caledonia (*australis*)	(21) 36·3–38·6	(14) 13·0–13·6	(16) 6·7–7·0	(13) 7·3–7·7	(14) 4·9–5·6	(10) 5·2–5·4

may be distinct from *australis,* while Maeda (1982) has raised *paululus* to specific rank and considered *shortridgei* its synonym. With these bats from the Philippines and Java, however, he associated small specimens from Rennell Island in the Solomon Islands to produce a somewhat anomalous distribution pattern for his proposed *M. paululus.* Koopman (1982) also recognised *paululus* as a distinct species in the islands off eastern Papua, the New Hebrides and Timor, although strongly tempted to treat *australis* and *paululus* as conspecific. The largest of specimens from Rennell Island and the New Hebrides, however, approach or overlap (Table 9) the smallest of *australis* from the Loyalty Islands and New Caledonia. Specimens from Timor are similar to *shortridgei* from Java but are sometimes slightly larger, as Goodwin (1979) pointed out.

Miniopterus australis tibialis (Tomes, 1858)

Vespertilio tibialis Tomes, 1858 : 126. Amboina I, Molucca Is.

SPECIMENS EXAMINED. C Sulawesi: ♂ BM(NH) 82.136 Taronggo, 1° 44′ S, 121° 40′ E; ♀ BM(NH) 82.137 R Ranu, 1° 51′ S, 121° 30′ E (in alcohol, skull of BM(NH) 82.136 lacking, of 82.137 extracted; coll. B. H. Gaskell, 'Operation Drake').

REMARKS. These specimens are the first of *M. australis* to be reported from Sulawesi, where on distributional grounds the species might be expected to occur. For the present they are referred to *M. a. tibialis* which is considered a probably distinct subspecies: they are similar in size (Table 9) to those from the Molucca Islands, New Guinea, the Aru Islands and Queensland discussed above.

Miniopterus pusillus pusillus Dobson, 1876

Miniopterus pusillus Dobson, 1876 : 162. Nicobar Islands.

SPECIMENS EXAMINED. Thailand: ♂, ♀ BM(NH) 78.2381–2382 Ban Huai Luang Cave, Chae Hom, Lampang (skins, skulls); ♀ BM(NH) 79.1422 Tham Hai Luang, Chag Hok, Lampang (in alcohol, skull extracted) (all presented by the Thai National Reference Collection, Bangkok).

Sumatra: ♂ JJW 15 Lian Penerukan, near Bohorok, Langkat (in alcohol, skull extracted; coll. J. J. Whitten).

W Java: ♀ BM(NH) 61.1781 Gua Tjibureum, Tjibodas, 2000 m; ♀ BM(NH) 61.1791 Klapanunggal, Tjileungsi (skins, skulls; coll. Earl of Cranbrook & P. Jauffret).

TYPE MATERIAL AND TYPE LOCALITY. Tate (1941*e*) gave the type locality of *Miniopterus pusillus* Dobson, 1876 as 'Madras, India' as did Ellerman & Morrison-Scott (1951) who also said 'But Wroughton gave Nicobar Islands as type locality'. Wroughton (1918) gave the type locality as 'Nicobars' and cited a specimen in the Indian Museum (No. 185) collected by Stoliczka as the lectotype.

The original description by Dobson provides no precise type locality but lists measurements of a specimen from the Nicobar Islands and of one from Madras. It includes a reference to an earlier paper (1871*c*) by Dobson in which he discussed specimens from the Nicobar Islands (collected by Stoliczka) that he referred to *M. australis* with some reservation. In his Catalogue of the Chiroptera in the collections of the British Museum (1878) Dobson listed the specimen from Madras and also others reputedly from the Philippine Islands under *Miniopterus schreibersii* var. a (i.e. *pusillus*) but gave measurements only for a Nicobarese specimen, taken evidently from his original work, and included the Andamans and Nicobars in the distribution of this form. Significantly, he did not indicate that the Madras specimen was the type. Clearly Dobson intended *pusillus* to apply to the Nicobarese specimens to which (1871*c*) he first drew attention, so that Wroughton's (1918) designation of a lectotype and type locality is justified. The choice of Madras as type locality and by implication of BM(NH) 52.8.12.8 from there as lectotype appears to rest only on its citation as the first specimen listed in Dobson's Catalogue (1878).

REMARKS. *Miniopterus pusillus* is similar in many respects to *M. australis* but may be distinguished from this species by its generally longer forearm that ranges from 39·3–45·5, longer tibia ranging from 16·5–22·0 and longer tail, its length varying from 43·5–52·0; its braincase is more globose, more elevated and higher, rising abruptly from the rostrum and is more elevated posteriorly, the height at the occiput nearly equal or equal to its height at the frontal; the rostrum is relatively short and is weak anteriorly when compared with that of *M. australis,* posteriorly wider and a little deeper; the upper canines are long and slender; as in *M. australis* m^1 has a well developed hypocone but the hypocone of m^2 is small or absent, the lingual shelf of this tooth more or less parallel-sided with no postero-internal projection.

The species is sympatric (chiefly as *M. p. macrocneme*) with *M. australis* over the eastern part of its range: although the two can generally be distinguished by the slightly greater external size of *pusillus* in locations where they occur together, such comparisons of specimens of each from different, widely separated localities can result in overlap. Dimensions of specimens in the collections of the British Museum (Natural History) appear in Table 10.

Besides specimens already noted, the collections in London include examples of *M. p. pusillus* from the Nicobar Islands (BM(NH) 90.6.20.2, 6.12.1.32–33) and from the island of Koh Lak, off the southeastern coast of Thailand (BM(NH) 17.2.6.4–7). Maeda (1982) referred BM(NH) 67.1810 from Bukit Cheras, near Panching, Kuantan, Pahang, Malaya to *pusillus,* but comparison suggests that more properly it represents *M. medius* with which it was first identified by Hill (1972). The specimens reputedly from the Philippine Islands listed by Dobson (1878) with, in parentheses, the locality 'Erumango' are BM(NH) A–C, not having been accessed formally or registered. They were obtained from Mr Hugh Cuming, a well known collector of Philippine mammals during the latter part of the last century. I have been unable to locate 'Erumango' in the Philippine Islands but there is an island called Eromango in the New Hebrides: Hoffman (1887) suggested that Dobson's designation was an error for New Hebrides. In cranial dimensions (Table 10) these specimens agree more closely with examples of *M. p. macrocneme* from New Guinea, the Solomon Islands and the New Hebrides rather than with more western specimens of this subspecies or with *M. p. pusillus* and also have the longer tibia characteristic of *macrocneme* rather than the shorter tibia of *pusillus.* Maeda (1982) also thought that they should be referred to *macrocneme.* A further specimen, BM(NH) 74.5.27.6, labelled 'Philippine Islands' and purchased from a Mr Salmin may represent *M. pusillus*, tentatively recorded from Baguio, Benguet Island by Taylor (1934).

The specimen reported here from Sumatra appears to be the first of *M. pusillus* to be recorded from that island, and the examples BM(NH) 61.1781 from Gua Tjibureum, Tjibodas and BM(NH) 61·1791 from Klapanunngal seem also to be the first of the species to have been recorded from Java. The Javan specimens were initially reported by Maeda (1982), who also referred others from Amboina, Ceram and the Kei Islands to *pusillus*, but these seem on comparison to be nearer to *macrocneme,* like those from New Guinea. On the other hand, specimens reported from Timor by Goodwin (1979) as *M. pusillus* have longer forearms like *macrocneme* but skulls that are similar in length to those of the western subspecies.

DISCUSSION. Recently accessed specimens from Thailand have made possible a wider assessment of *M. pusillus* than was hitherto feasible in London, although the available material remains inadequate for any detailed analysis of subspecific variation. In particular the newly acquired material has demonstrated that the limited number of Siamese specimens hitherto in the collections should not be referred to *M. australis* as once they were, but instead to *M. pusillus* which itself is specifically distinct.

Table 10 Measurements of *Miniopterus pusillus* (number of specimens examined in parentheses).

	Length of forearm	Length of tibia	Condylobasal length	Width of braincase	Mastoid width	m^3–m^3	c–m^3
M. p. pusillus							
Nicobar Is	(3) 39·3–40·1	(3) 16·8–17·6	(3) 12·7–12·9	(3) 7·0–7·2	(3) 7·5–7·6	(3) 5·5–5·6	(3) 5·0–5·1
Madras	(1) 42·5	(1) 18·4	—	(1) 7·4	—	—	(1) 5·3
Thailand	(7) 40·7–42·6	(7) 16·5–18·4	(7) 12·8–13·3	(7) 7·2–7·4	(5) 7·5–7·9	(6) 5·5–5·6	(7) 5·0–5·2
Sumatra	(1) 41·8	(1) 17·5	(1) 13·3	(1) 7·4	(1) 7·9	(1) 5·6	(1) 5·3
Java	(1) 42·4	(1) 18·0	(1) 13·3	(1) 7·3	(1) 7·6	(1) 5·6	(2) 4·9–5·2
M. p. macrocneme							
Sulawesi	(5) 43·1–45·0	(5) 18·8–19·8	(5) 12·9–13·2	(5) 7·2–7·4	(5) 7·5–7·7	(5) 5·4–5·5	(5) 5·0–5·1
Amboina I, Ceram I	(7) 40·5–43·6	(7) 17·5–19·2	(5) 13·1–13·4	(6) 7·0–7·4	(5) 7·3–7·8	(6) 5·6–5·7	(3) 5·2–5·3
Kei Is	(5) 40·5–42·1	(5) 17·2–17·9	(3) 12·9–13·3	(3) 7·0–7·3	(3) 7·4–7·6	(3) 5·5–5·7	(3) 5·2–5·4
Timor I (ex Goodwin, 1979)	(58) 41·2–44·1	—	(6) 12·6–12·9	—	(6) 7·6–7·8	(6) 5·4–5·6	(6) 5·0–5·1
Batchian I	(1) 41·8	(1) 19·2	—	—	—	—	—
New Guinea	(21) 40·6–45·5	(19) 17·2–19·2	(2) 13·7–14·1	(2) 7·3–7·6	(1) 8·2	(2) 5·7	(2) 5·5
San Christobal I, Solomon Is	(2) 40·9–43·1	(2) 18·1–18·9	(1) 13·6	(2) 7·1–7·3	(2) 7·3–7·8	(2) 5·7–5·8	(2) 5·3–5·4
New Hebrides	(48) 40·5–43·5	(48) 18·5–20·0	(1) 13·9	(1) 7·3	(1) 8·0	(1) 5·9	(1) 5·6
'Erumango' (see text)	(3) 41·8–42·2	(3) 18·9–19·2	(2) 13·6–13·8	(2) 7·3–7·4	(2) 8·0	(2) 5·9	(2) 5·5–5·6
New Caledonia	(2) 40·7–41·7	(2) 18·2–18·6	—	—	—	—	—
Loyalty Is	(1) 40·7	—	(1) 13·2	(1) 7·1	(1) 7·8	(1) 5·6	(1) 5·3

Miniopterus pusillus macrocneme Revilliod, 1914

Miniopterus macrocneme Revilliod, 1914 : 360. New Caledonia and Loyalty Islands.

Specimens examined. C Sulawesi: ♂, ♀ BM(NH) 83.138–139 R Ranu, 1° 51′ S, 121° 40′ E (in alcohol, skulls extracted; coll. B. H. Gaskell, 'Operation Drake').

New Hebrides: 5 ♂♂, 5 ♀♀, 1 undetermined BM(NH) 73.1502–1512 'Pig Cave', Harris Plantation, N coast Efate I, 40 m; ♂, 2 ♀♀ BM(NH) 73.1513–1515 'Pig Cave', Narabut Camp, Efate I, 800 ft; 2 ♂♂, 2 ♀♀ BM(NH) 73.1516–1519 'Pig Cave', Efate I; 2 ♂♂, 2 ♀♀ BM(NH) 73.1520–1523 Paul's bungalow site, near 'Bethel', Tanna I, sea level; 2 ♂♂ BM(NH) 73.1524–1525 Siwi, Tanna I; 2 ♂♂, 2 ♀♀ BM(NH) 73.1526–1529 Arvat, E coast Erromanga I, sea level; ♂, ♀ BM(NH) 73.1530–1531 Womban Wovoula Cave, Abouanatori village, Malo I, 50 m; ♂, ♀ BM(NH) 73.1532–1533 Abouanatori village; ♂ BM(NH) 73.1534 Aouta, Aore I; ♂, ♀ BM(NH) 73.1535–1536 Limboh, near Litzlitz, Port Stanley Bay, Malekula I; ♀♀ BM(NH) 73.1537–1541 Lomboh Cave, near Litzlitz, 5 m; 3 ♂♂, 2 ♀♀ BM(NH) 73.1542–1546 Lipelip Cave, Amok, Malekula I, 440 m (all in alcohol; obtained Earl of Cranbrook, Royal Society Expedition to New Hebrides, 1971).

Remarks. The first record of *M. pusillus* from Sulawesi was provided by Hill (1974) who reported specimens (as *M. medius macrocneme*) from Wawondula in the southern part of the island. For the present Sulawesian specimens are referred to *M. p. macrocneme* but the total of material available is quite inadequate for the proper evaluation of subspecies or their boundaries. However, these specimens and those obtained earlier have the long tibiae (Table 10) usual in this more eastern subspecies.

Miniopterus pusillus macrocneme occurs with *M. australis* throughout the range of the subspecies but may be distinguished by the characters noted above under *M. p. pusillus*. According to Revilliod (1914) *macrocneme* may be differentiated from *australis* by the shape of the tragus, which in the latter he stated projects anteriorly in its distal part, with a nearly horizontal, irregularly dentate upper margin while in *macrocneme* the tragus is less strongly projected forward and there is no well marked dentate upper margin. The anterior projection of the upper part of the tragus is more pronounced in specimens of *australis* from New Caledonia and the Loyalty Islands (whence Revilliod drew his observations) and the New Hebrides than in those from more westerly locations and in such examples the tragus has a nearly horizontal upper margin, sometimes slightly dentate, both features that disappear from more westerly populations. Neither has therefore any extensive diagnostic value.

Discussion. Hill (1971*a*, 1974) considered *macrocneme* (an eastern form extending apparently from Sulawesi east to the New Hebrides, New Caledonia and the Loyalty Islands) conspecific with *medius* Thomas & Wroughton, 1909 from Java but Peterson (1981*b*) has suggested that *macrocneme* represents the *pusillus* species group and that *medius* belongs to the *fuscus* group of species. Newly acquired specimens have established *medius* in southern Thailand in near sympatry with *pusillus*, while others whose skulls have become available recently have shown it to occur sympatrically with *pusillus* in Java; moreover the additional material has suggested that *medius* must be considered specifically distinct, and that *pusillus* and *macrocneme* are most probably conspecific.

Maeda (1982) seems uncertain in his group allocation of *macrocneme* but finally places it as a species in the *fuscus* group along with *M. fuscus* and *M. medius*. However, the discriminatory ratios given by Maeda for *macrocneme* overlap considerably into those that he gives for the *pusillus* group, and direct comparison of specimens reveals close similarities of structure. For this reason I agree with Peterson (1981*b*) that *macrocneme* and *pusillus* should be associated, and incline further to the view, used here, that they are conspecific.

Miniopterus medius Thomas & Wroughton, 1909

Miniopterus medius Thomas & Wroughton, 1909 : 382, Kalipoetjang, Tji-Tandoei R, Java.

Specimens examined. Thailand: ♂ BM(NH) 78.1424 Ban Kok Chang, Nakhon Sri Thamrat (in alcohol, skull extracted; presented by Thai National Reference Collection).

Table 11 Measurements of *Miniopterus medius* and *M. fuscus* (numbers of specimens examined in parentheses).

	Length of forearm	Condylobasal length	Braincase width	Mastoid width	m^3–m^3	c–m^3
M. medius						
Thailand	(1) 41·9	(1) 14·3	(1) 7·5	(1) 8·2	(1) 6·4	(1) 6·0
Malaya	(4) 42·2–43·3	(1) 13·8	(1) 7·7	(1) 8·1	(1) 5·9	(1) 5·4
Pulau Kaban, Johore Archipelago	(5) 41·3–42·6	(5) 13·8–14·1	(5) 7·4–7·8	(5) 8·0–8·3	(4) 5·8–5·9	(5) 5·5
Java	(13) 40·8–45·0	(9) 14·0–14·5	(10) 7·3–7·6	(10) 7·7–8·4	(9) 6·1–6·5	(10) 5·7–6·0
New Guinea	(1) 47·5	(1) 14·4	(1) 7·5	(1) 8·4	(1) 6·1	(1) 5·7
M. fuscus (*yayeyamae*)						
Okinawa I, Ishigaki Is	(13) 38·0–44·5	(4) 13·8–14·1	(4) 7·4–7·5	(4) 7·9–8·2	(8) 5·9–6·3	(6) 5·4–5·8

Malaya: ♂, ♀ BM(NH) 69.1250–1251 Base of Gunong Ledang (=G. Ophir), Johore, 2° 21′ N, 102° 39′ E; ♂ BM(NH) 75.1296 Sungei Kelambang Camp, Ulu Setiu, Besut, Trengganu, c. 5° 25′ N, 102° 42′ E (all in alcohol; obtained by the Earl of Cranbrook).

Java: 3 ♂♂, 4 ♀♀ BM(NH) 61.1766–1768 (in alcohol, skulls of BM(NH) 61.1766, 61.1768 extracted), BM(NH) 61.1782–1783 (skins, skulls), BM(NH) 61.1784–1785 (in alcohol, skulls extracted) Klapanunngal, Tjileungsi, 280 m (coll. Earl of Cranbrook & P. Jauffret).

Papua New Guinea: ♀ BM(NH) 80.657 Mt Kainoi, Wau, 7° 19′ S, 146° 44′ E (in alcohol, skull extracted; coll. B. H. Gaskell, 'Operation Drake').

REMARKS. There appear to be no definitive published records of *M. medius* from the area east of Java. Baker & Bird (1936) recorded *medius* from Espiritu Santo Island in the New Hebrides but two of their specimens still available (BM(NH) 36.4.8.1–2) in fact prove to be *M. pusillus macrocneme.* Similarly, the specimens from Papua New Guinea reported as *medius* by McKean (1972) seem likely to represent *macrocneme* (Koopman, 1982 thinks MH 984 from Putei perhaps referable to *M. schreibersii*): certainly examples (BM(NH) 50.1802–1803) from Tomba, in the Hagen Range, Papua New Guinea, first reported by Laurie (1952) as *M. schreibersii blepotis* but later thought to represent *medius* in fact belong to *macrocneme* while another (BM(NH) 39.1403) from Nadimo Valley, The Gebroeders, Weyland Range, West Irian although previously identified as *medius* is also *macrocneme.* These specimens were among those leading Hill (1971*a*) to consider *macrocneme* conspecific with *medius.* The specimen reported here from Mount Kainoi provides evidence of near sympatry between *medius* and *M. pusillus macrocneme* in eastern New Guinea: as pointed out above, *medius* also occurs near or with *M. p. pusillus* in Thailand and Java.

Measurements of *M. medius* in the collections of the British Museum (Natural History) appear in Table 11. The largest of *M. pusillus* equal or overlap the smallest of *M. medius* in some respects but the two can be distinguished by the generally larger skull and more massive teeth of the latter. Equally, the largest of *medius* approach or overlap the smallest of *M. schreibersii* in some dimensions but *medius* has a narrower skull and braincase: in any event, there appears to be no overlap when specimens from the same general area are compared. Although the example of *medius* recorded here from New Guinea has a forearm that is considerably longer than the forearms of *medius* from Java or from the more western parts of its range, the specimen agrees very closely with Javan examples both in the structure and the dimensions of its skull and teeth.

DISCUSSION. Peterson (1981*b*) suggested that *medius* belonged to the *fuscus* species group, an opinion confirmed by Maeda (1982). An examination of the holotype (BM(NH) 2.10.7.3) of *M. fuscus* Bonhote, 1902 from Okinawa Island, Liu Kiu Islands shows that in all relevant features it is clearly allied to *M. medius* and is also dimensionally very similar. Possibly with or including *yayeyamae* Kuroda, 1924 from Ishigaki Island, also in the Liu Kiu Islands, it may be a northern representative of *medius*: certainly on cranial features and size it has no connection with *M. schreibersii* (Kuhl, 1819) as was suggested by Tate (1941*e*) or by Ellerman & Morrison-Scott (1951) who, perhaps influenced by Tate's remark that it was virtually equal to *blepotis* (Temminck, 1840) and to *eschscholtzii* (Waterhouse, 1845) synonymised both *fuscus* and *yayeyamae* with *M. schreibersii blepotis.*

Miniopterus schreibersii blepotis (Temminck, 1840)

Vespertilio blepotis Temminck, 1840: 212, pl. 53, figs 1, 2. Java, Timor and Amboina. Lectotype tentatively designated and type locality restricted to Java by Tate (1941*e*): Maeda (1982) has designated a further lectotype and a series of paralectotypes (including the specimen selected by Tate) from Java.

SPECIMEN EXAMINED. C Sulawesi: ♂ BM(NH) 82.141 Taronggo, 1° 44′ S, 121° 40′ E (in alcohol, skull extracted; coll. B. H. Gaskell, 'Operation Drake').

REMARKS. This appears to be the second record of *M. s. blepotis* from Sulawesi, Tate (1941*e*) having recorded a specimen from the southern part of the island. In most dimensions (Table

12) it agrees with specimens from western Java but has a longer forearm and longer skull similar to those of specimens from Amboina Island. These latter were referred to a newly described species *M. oceanensis* (see below) by Maeda (1982), who has made an extensive study of Eurasian and Australasian *Miniopterus* and has provided a key. Use of this key, which relies heavily on proportional ratios for discrimination, identifies the Sulawesian specimen to the *fuliginosus, blepotis* or *schreibersii* groups and thence to *M. fuliginosus* or *M. eschscholtzii* if the ratio forearm length/greatest length of skull is employed (and from there to *M. fuliginosus* on forearm length and the ratio m^3–m^3/condylobasal length) but to *M. blepotis* if the ratio mastoid width/greatest length of skull is used.

Measurements of BM(NH) 82.141: length of forearm 46·7; greatest length of skull 15·9; condylobasal length 15·5; condylocanine length 14·5; least interorbital width 3·9; zygomatic width 8·9; width of braincase 7·9; mastoid width 8·6; c^1–c^1 (alveoli) 4·5; m^3–m^3 6·8; c–m^3 6·2; length complete mandible from condyles 11·5; length right ramus from condyle 11·5; c–m^3 6·8.

Discussion. Until recently the conventional view of *M. schreibersii* (Kuhl, 1819) of eastern Asia and Indo-Australia included those forms with forearm lengths ranging from 44 or slightly less to 50 or thereabouts, the condylobasal length of the skull varying from about 14·5 to a maximum of some 16, the exception being *M. s. magnater* Sanborn, 1931 from New Guinea which exceeds these upper limits. Peterson (in Goodwin, 1979) considered *magnater* to represent a distinct species while Kobayashi *et al.* (1980) have also raised *magnater* to specific rank, recording it with *schreibersii* from Sabah in northern Borneo. More recently Maeda (1982) has described the Sabah population initially referred to *magnater* as a new species, *M. macrodens,* associating with it specimens from a wide variety of localities from Hong Kong to South Australia. It is discussed in more detail below[1]. Tate (1941*a*) suggested that the small forms *fuscus* Bonhote, 1902 from Okinawa Island, Liu Kiu Islands and *yayeyamae* Kuroda, 1924 from Ishigaki-Mura, Ishigaki Island, also in the Liu Kiu Islands might be synonymous representatives of *M. schreibersii,* equal to *M. s. blepotis* with which both were synonymised by Ellerman & Morrison-Scott (1951). Specimens in the British Museum (Natural History), including the holotype of *fuscus,* show clearly that these do not represent *M. schreibersii* but instead are near to *M. medius* of Thailand, Malaya, Java and New Guinea, as Maeda (1982) suggests, and of which they may be northern representatives. Of these, *fuscus* is the earliest name.

The collections of the British Museum (Natural History) show that in fact the concept of *M. schreibersii* hitherto widely accepted includes two sympatric forms, as the conclusions of Peterson (1979) and Kobayashi *et al.* (1980) imply, and as Maeda (1982)[1] has established, in part from the same collections. One, regarded here as *M. schreibersii*, is smaller, with a relatively narrower palate (Table 12). In eastern Asia and in the Indo-Australian region it occurs from Afghanistan, India and Sri Lanka to Japan, the Philippine Islands and east to the Solomon Islands and Australia. The other, consisting of larger examples, with longer skull and toothrows and wider palate, but with the forearm on the whole only very slightly longer (Table 13), is represented in the collections from Hong Kong, Burma, Thailand, Malaya, Sumatra and Java[1]. Such specimens represent *M. macrodens* Maeda, 1982: they agree closely in structure and size with *M. magnater* from New Guinea and are discussed more fully under that species. All have been referred to *M. schreibersii* in the past when this species was presumed to embrace a greater size range to include *magnater* as a subspecies (e.g. BM(NH) 67.217 from Pahang by Hill (1972)) or before then (e.g. BM(NH) 9.1.5.460–461 from Java by Thomas & Wroughton (1909) who in allocating these to *blepotis* remarked upon their long forearms in comparison with other Javanese specimens) like those reported and measured from Hainan by Allen (1938*b*), which seem on size to be very similar to these large examples and are referred without examination to *macrodens* by Maeda (1982). Specimens from Java reported as *blepotis* by Sody (1930) are very large for this form and much nearer in size to the large examples from Soekaboemi (BM(NH) 9.1.5.460–461) noted above

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[1] See Addendum, p. 208

Table 12 Measurements of *Miniopterus schreibersii** (numbers of specimens examined in parentheses).

	Length of forearm	Condylobasal length	Width of braincase	Mastoid width	m^3–m^3	c–m^3
Afghanistan; India	(19) 46·2–48·5	(10) 14·6–15·3	(11) 7·7–8·2	(10) 8·4–9·0	(11) 6·3–6·8	(11) 5·8–6·2
Burma	(1) 48·0	(1) 15·2	(1) 8·1	(1) 8·7	(1) 6·8	(1) 6·2
Thailand (*haradai*, ex Maeda, 1982)	(4) 42·5–43·7	(4) 14·7–15·3	(4) 7·5–8·1	(4) 8·2–8·5	(4) 6·3–6·5	(4) 5·9–6·2
Vietnam	(7) 46·7–48·4	(6) 14·7–15·5	(5) 7·7–8·2	(5) 8·5–9·1	(6) 6·5–6·8	(6) 5·8–6·2
Fukien, China	(1) 47·3	(1) 15·6	(1) 8·2	(1) 8·8	(1) 6·6	(1) 6·2
Chihli, China	(15) 45·9–49·0	(11) 14·9–15·6	(10) 7·9–8·2	(11) 8·8–9·0	(15) 6·4–6·8	(15) 5·9–6·3
Japan	(14) 44·8–47·9	(10) 14·5–15·4	(10) 7·5–8·0	(10) 8·3–8·8	(10) 6·5–6·7	(10) 5·8–6·2
Philippine Is	(2) 44·7–45·5	(1) 14·6	(1) 7·6	(1) 8·4	(1) 6·7	(1) 6·0
Malaya	(1) 44·8	(1) 15·0	(1) 8·1	(1) 8·7	(1) 6·6	(1) 6·0
Sumatra	(2) 47·0, 48·5	(1) 15·2	(1) 8·3	(1) 8·6	(1) 6·8	(2) 6·2
Java	(16) 43·6–45·8	(14) 14·8–15·6	(14) 7·8–8·2	(13) 8·3–8·7	(15) 6·6–6·9	(15) 5·9–6·3
Java (*ravus*, ex Sody, 1930)	(2) 43	—	(2) 8·2–8·5	—	—	(2) 6·1–6·4
Sulawesi	(1) 46·7	(1) 15·5	(1) 7·9	(1) 8·6	(1) 6·8	(1) 6·2
Amboina	(3) 45·5–46·5	(3) 15·4–15·9	(3) 7·8–8·2	(3) 8·5–9·1	(3) 7·1–7·2	(3) 6·3–6·4
Kei Is	(6) 44·3–44·9	(5) 14·9–15·4	(5) 7·6–8·0	(5) 8·3–8·8	(5) 6·6–7·0	(5) 6·1–6·3
New Guinea	(3) 47·4–47·9	(3) 15·2–15·6	(3) 8·0–8·2	(3) 8·3–8·9	(3) 7·0–7·3	(2) 6·2
Timor I (ex Goodwin, 1979)	(20) 46·6–49·7	(3) 15·5–15·8	—	(3) 8·8–9·0	(3) 7·2–7·3	(3) 6·5–6·7
E Australia (*oceanensis*)	(63) 45·4–48·6	(17) 15·1–15·9	(18) 8·0–8·4	(18) 8·7–9·2	(19) 6·8–7·2	(22) 6·2–6·4
N Australia (*orianae*)	(11) 43·1–46·7	(8) 15·0–15·5	(7) 7·7–8·1	(8) 8·3–8·8	(6) 6·2–6·8	(7) 5·7–6·0
New Ireland	(2) 46·1–46·4	(2) 14·6–14·8	(2) 7·4–7·7	(2) 8·2–8·3	(2) 6·6–6·7	(2) 6·1
Rennell I, Solomon Is	(7) 45·7–48·4	(8) 14·6–15·7	(11) 7·6–8·0	(10) 8·1–8·7	(10) 6·5–7·0	(9) 5·9–6·4

*Possibly valid subspecies are discussed in the text.

Table 13 Measurements of *Miniopterus magnater* and *M. bismarckensis* (number of specimens examined in parentheses).

	Length of forearm	Condylobasal length	Width of braincase	Mastoid width	m^3–m^3	c–m^3
M. m. macrodens						
Hong Kong	(1) 51·0	(1) 16·7	(1) 8·7	(1) 9·7	(1) 7·5	(1) 6·6
Yunnan	(1) 51·0	—	—	—	(2) 7·1	(2) 6·4–6·5
Burma	(1) 49·4	(1) 16·5	(1) 8·5	(1) 9·7	(1) 7·4	(1) 6·7
Thailand	—	(2) 15·9–16·1	(2) 8·3–8·5	(2) 8·9–9·1	(2) 7·3–7·4	(2) 6·5
Koh Lak I, off SE Thailand	(1) 50·1	(1) 16·0	(1) 8·3	(1) 9·1	(1) 7·4	(1) 6·5
Malaya	(2) 49·4–50·8	(1) 16·3	(1) 8·5	(1) 9·3	(1) 7·4	(1) 6·5
Sumatra	(4) 48·8–51·0	(1) 17·4	(1) 8·4	(1) 9·2	(1) 7·6	(1) 7·2
Java	(2) 50·1–50·4	(2) 15·8–16·1	(2) 8·3–8·4	(2) 9·1–9·2	(2) 7·1–7·3	(1) 6·7
M. m. magnater						
New Guinea	(20) 48·5–51·7	(3) 16·7–17·0	(5) 8·3–8·6	(3) 9·2–9·4	(5) 7·5–7·9	(5) 6·8–7·0
*M. bismarckensis**						
Manus I, Bismarck Archipelago	(3) 44·4–46·4	—	—	—	(2) 7·2, 7·1	(2) 7·1, 7·3

*see text.

and are also referred to *macrodens* by Maeda, while *M. ravus* Sody, 1930, described concurrently, seems on measurements to be close to *blepotis*, to which Maeda refers its holotype specimen.

Maeda (1982) has proposed wide ranging changes in the classification of *Miniopterus* from Eurasia and especially Indo-Australia, many closely affecting that part of the genus formerly held to include *schreibersii, blepotis* and a number of other related taxa. These changes may be briefly summarized by comparison with the pre-existing classification, chiefly derived from Tate (1941*e*) and from Ellerman & Morrison-Scott (1951), excluding purely Eurasian taxa and also *fuscus* and its allied forms:

Previous concept	**Maeda (1982)**
M. schreibersii pallidus (Afghanistan)	*M. schreibersii*
M. schreibersii fuliginosus (Afghanistan to S China, Japan)	*M. fuliginosus*
M. schreibersii chinensis (N China)	*M. fuliginosus*
M. schreibersii eschscholtzii (Philippines)	*M. eschscholtzii*
M. schreibersii blepotis (in part, Malaysia)	*M. blepotis*
M. schreibersii blepotis (in part, Moluccas to Australia, Solomon Is)	*M. oceanensis*
M. schreibersii orianae (N Australia)	*M. eschscholtzii*

To these he adds a further newly described species, *M. haradai* Maeda, 1982 from southern Thailand.

As can be seen, the concept of one widely ranging polytypic species is replaced by Maeda (1982) by five species. Moreover, the arbitrary statistical treatment used in this study removes *oceanensis,* applied to specimens that formerly were referred to *M. s. blepotis,* to the *magnater* subgroup of the *fuliginosus* group as Maeda defines them, while *blepotis* and *eschscholtzii* form another group (the *blepotis* group), and *schreibersii* yet a third. There is no doubt that the statistical analysis of metrical characters made by Maeda has identified and codified many, if not all of the parameters used hitherto in the identification of the forms of *Miniopterus* in Eurasia and Indo-Australia. The allocation of taxonomic rank to the groupings so characterised, however, seems very arbitrary and biased rather more heavily towards the interpretation of metrical data than towards morphological and zoogeographical considerations. Thus Maeda admits (p. 21) that there is no clear difference in general morphological characteristics between all of the species of the *fuliginosus* group (i.e. *magnater, macrodens, oceanensis, fuliginosus*) and those of the *blepotis* group (i.e. *blepotis, eschscholtzii, haradai*), although he pointed out that there are some conspicuous differences between the *magnater* subgroup (*magnater, macrodens, oceanensis*) and the *blepotis* group, and also between the *fuliginosus* subgroup (*fuliginosus*) and the *blepotis* group. These statements appear at least superficially to contain a contradiction. A comparison of Maeda's distribution maps (figs 34, 35) for these taxa shows that (excluding *magnater* and *macrodens,* discussed below) each replaces another in characteristic fashion across the region and that none is sympatric although *schreibersii* and *fuliginosus* are nearly so in Afghanistan. Maeda himself (p. 28) stated that according to his conclusions 'In many miniopterine bats, the species belonging to the same group are usually allopatric in distribution'.

The interpretation by Maeda produces a number of curious distributional anomalies. Thus *oceanensis* is said to occur in Australia, the Solomon Islands and tentatively in Burma and Yunnan. However, the specimen from Burma (BM(NH) 67.2323) has a molar width (m^3–m^3) of 6·8 and so, from his key, falls into the *fuliginosus, blepotis* or *schreibersii* groups, while its toothrow (i^1–m^3) length of 7·3 and mastoid width of 8·7 take it to the *fuliginosus* subgroup or the *blepotis* group. The length of the forearm is 48·0 and the greatest skull length 15·4, the condylobasal length 15·2: these values take it further in the key to *fuliginosus.* Specimens from Yunnan (BM(NH) 12.7.25.4–5) have damaged skulls from which only the palatal measurements can be drawn but these (Table 13) agree closely with those of *macrodens* from Thailand and Koh Lak Island.

A further anomaly is to be found in the distribution of *eschscholtzii,* as it is proposed by Maeda. According to this author, it occurs in the Philippines whence it was originally named, in northern and South Australia where in northern Australia according to Maeda it displaces the name *orianae* Thomas, 1922, and on San Christobal Island in the Solomon Islands. The South Australian record is drawn from Leche (1884) who originally identified the material as *M. schreibersii blepotis.* The remaining Australian examples were originally referred to *M. s. orianae*: those from San Christobal to *M. s. blepotis* by Hill (1971*a*). However, the Australian examples referred initially to *orianae* do not always meet the criteria laid down in Maeda's key for *eschscholtzii,* some (BM(NH) 22.10.8.2–3, 29.1.9.1) keying more appropriately to *blepotis* and another (BM(NH) 29.1.9.3) producing some ratios more appropriate to his parameters for *fuliginosus.* Similar considerations apply to specimens (BM(NH) 54.901–903) from Rennell Island, from San Christobal Island (BM(NH) 67.1882–1883, 67.1885–1888) and one (BM(NH) 91.8.20.2) from Bugota Island, all in the Solomon Islands.

A condition such as this might be expected within the distribution of a widespread polytypic species with populations scattered over numerous islands of different size: some populations at least, even on widely distant islands, might be expected to resemble each other in some features of size and proportion. A further point is that of the San Christobal series (BM(NH) 67.1882–1888) identified formerly as *blepotis,* one example BM(NH) 67.1884) is determined by Maeda as *oceanensis,* while the remainder are referred to *eschscholtzii.* This is apparently because this specimen has a slightly wider palate (m^3–m^3 7·0) than the others (m^3–m^3 6·6–6·9) and thus keys to the *magnater* subgroup of Maeda (and hence to *oceanensis*) rather than to the *schreibersii, fuliginosus* or *blepotis* agglomerations, as do the remainder of the series.

In Amboina Maeda (1982) records *blepotis* and *oceanensis* sympatrically. However, members of the one series of specimens from Amboina Island in the British Museum (Natural History) (BM(NH) 10.7.24.24–26) have very slightly wider palates and are very slightly larger (Table 12) than specimens from the Kei Islands (BM(NH) 10.3.1.30, 10.3.1.70–71, 74, 94, 95) that otherwise they closely resemble. Consequently like BM(NH) 67.1884 from San Christobal they key to *oceanensis* while examples from the Kei Islands are taken to *blepotis,* yet as can be seen (Table 12) actual differences are very small. The Amboina specimens that Maeda refers to *blepotis* are in the Rijksmuseum van Natuurlijke Historie: they include one skull (his population 47, p. 92). According to his table of measurements (p. 127) this skull has a mastoid width of 7·0: it should therefore key out to his *magnater* subgroup (including *oceanensis*) rather than to *blepotis* to which he refers it.

I am led to the conclusion that *oceanensis* from Amboina, New Guinea, the Solomon Islands and eastern Australia should be considered a subspecies of *M. schreibersii* as here understood, rather than be associated with *M. magnater.* Those from Timor reported as *magnater* by Goodwin (1979) seem on size to be more properly referred to *M. s. oceanensis*: all are linked to the smaller, more westerly populations by those from the Kei Islands. The collections of the British Museum (Natural History) contain only a single example (BM(NH) 78.1.21.6) of *M. schreibersii* from New Guinea: Maeda (1982) refers it to *oceanensis* and records no other New Guinea specimen. However, I have examined two further examples (♂, ♀ BBM 55803, 55893) from the Bernice P. Bishop Museum, Honolulu, that also come from New Guinea. These are from Danowaria Cave, near Fak Fak, Fak Fak District, West Irian, at 25 m.

In view of the various considerations advanced above, I have retained the view that all of these medium-sized *Miniopterus* in Indo-Australia (excluding *magnater* and *macrodens*) form a polytypic species extending from Afghanistan to Japan, the Philippine Islands, the Solomon Islands and Australia. If allied to *schreibersii* of Eurasia then it extends westward into western Europe and into Africa: there seems at present no reason to consider the Asiatic and Indo-Australian populations distinct from *schreibersii* unless for example extensive sympatry can be demonstrated in Afghanistan where *M. s. pallidus* is found at Kandahar and *M. s. fuliginosus* at Jalalabad. In eastern Asia and in the Indo-Australian region this species occurs from Japan (*japoniae* Thomas, 1906*b*) and northeastern China (*chinensis* Thomas, 1908*a*) to southern China and Vietnam (*parvipes* Allen, 1923), India and Sri Lanka (*fuliginosus* (Hodgson, 1835)), the Philippine Islands (*eschscholtzii* (Waterhouse, 1845)), Malaya and Sumatra east to Sulawesi and Java (*blepotis* (Temminck, 1840)), the Molucca Islands, New Guinea, the Solomon Islands and eastern Australia (*oceanensis* Maeda, 1982), and in northern Australia (*orianae* Thomas, 1922*c*). Maeda (1982) associated *oceanensis* with *M. magnater* but as already pointed out specimens referable to this form seem clearly on comparison to represent the smaller and not the larger of the two similar sympatric species although they are often rather larger than most of *M. schreibersii*. No specimens from Thailand have been examined. *Miniopterus haradai* Maeda, 1982, from the southern part of the country, however, is very close in size (Table 12) to specimens referred to *M. schreibersii* from Vietnam and Malaya and may well be its local representative. For the present I would consider it to be a subspecies of *M. schreibersii*.

Miniopterus magnater magnater Sanborn, 1931

Miniopterus schreibersii magnater Sanborn, 1931 : 26. Marienberg, 40 miles up Sepik R, Papua New Guinea.

Specimens examined. Papua New Guinea: ♂ BM(NH) 78.893 No further locality (in alcohol; coll. P. A. Morris); 2 ♂♂, 8 ♀♀ BM(NH) 80.658–667 Mt Kainoi, Wau, Morobe, 7° 31′ S, 146° 43′ E; 2 ♂♂, 2 ♀♀ BM(NH) 82.153–156 Cave at Avi, Mt Hagen (all in alcohol; coll. B. H. Gaskell, 'Operation Drake').

Remarks. These specimens agree with *M. m. magnater* as it is represented by the limited sample hitherto in the collections of the British Museum (Natural History).

Discussion. The status of this species has been briefly discussed above. It is distinguished from *M. schreibersii* by its generally longer forearm, larger skull, wider braincase and wider palate. Maeda (1982) defined a *magnater* subgroup in some detail, but in including *oceanensis* removed the basis of size characters in the definition of *magnater*, this newly recognised taxon being little larger than other Indo-Australian specimens of *M. schreibersii* as here understood but having the palate very slightly widened. It is based on specimens formerly allocated to *M. schreibersii* to which it is here allocated as a subspecies.

Specimens from localities from Hong Kong to Sumatra and Java have been briefly mentioned under *M. schreibersii blepotis* to which they were once referred. With the exception of some of the Thai and Sumatran examples they have been allocated to *macrodens* by Maeda (1982) when describing that form. In detail these come from Hong Kong (BM(NH) 65.1019, Old Mine, Silver Mine Bay), Burma (BM(NH) 32.11.1.3, Nam Tisang), Thailand (BM(NH) 79.1425–1426, no further locality; (BM(NH) 17.2.6.3, Koh Lak Island, off southeastern Thailand), Malaya (BM(NH) 67.217, Pine Tree Hill, Fraser's Hill, Pahang), Sumatra (BM(NH) 0.8.2.11–14, Balighe) and Java (BM(NH) 9.1.5.460–461, Soekaboemi, Preanger)[1]. The majority is male and all are fully adult or even old.

These specimens agree closely in structure and size (Table 13) with *M. magnater* from New Guinea. According to Maeda (1982) *M. macrodens* differs from *magnater* in shorter condylobasal length, shorter upper toothrow and narrower palate. A study of Maeda's measurements shows that while *macrodens* is generally smaller in these respects than *magnater*, the largest of the former overlaps the smallest of the latter, a circumstance apparent in the specimens in London. Indeed, in some respects one Sumatran example of *macrodens* exceeds *magnater* from New Guinea, yet in others falls at the lowest part of the range of the New Guinea material. For this reason I consider *macrodens* Maeda, 1982 a subspecies of *M. magnater*, distributed from Hong Kong and Burma at least to Sumatra and Java. Maeda (1982) refers specimens without skulls from Amboina to *macrodens* but their forearm length (populations 43, 45, pp. 110, 111) are compatible either with this form or with *magnater*: specimens from Mount Flinders, South Australia, also referred to *macrodens* by Maeda (population 81, pp. 114, 134) also have forearms of a similar length but the sole skull measured agrees with *macrodens*.

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[1] See Addendum, p. 208.

Miniopterus tristis celebensis Peterson, 1981

Miniopterus tristis celebensis Peterson, 1981*b* : 841. Luwu, Wawondula, Sulawesi, 02° 38′ S, 121° 21′ E.

SPECIMENS EXAMINED. C Sulawesi: ♂♂ BM(NH) 82.142–143 R Ranu, 1° 51′ S, 121° 30′ E (in alcohol, skulls extracted; coll. B. H. Gaskell, 'Operation Drake').

REMARKS. These specimens clearly support Peterson's contention that the Sulawesian population of *M. tristis* is distinct from that of the Philippine Islands, from which Sulawesian examples may be distinguished by their larger size and especially by the greater length of the forearm and metacarpals. The examples recorded here bring the known total of specimens of *M. t. celebensis* to four. Measurements: (BM(NH) 82.142, 82.143): length of forearm 57·5, 57·1; III^{m} 54·2, 53·3; IV^{m} 51·9, 50·4; V^{m} 44·3, 44·0; length of tibia 24·1, 23·8; greatest length of skull 19·6, 19·7; condylobasal length 19·3, 19·2; condylocanine length 18·4, 18·4; least interorbital width 4·1, 4·3; zygomatic width 11·0, —; width of braincase 8·9, 9·0; mastoid width 10·0, 10·1; c^1–c^1 (alveoli) 6·0, 6·1; m^3–m^3 8·8, 8·8; c–m^3 8·3, 8·1; length of complete mandible from condyles 14·6, 14·7; length of right ramus from condyle 15·1, 15·1; c–m^3 8·8, 8·7.

DISCUSSION. Hill (1971*a*) in recording *M. tristis* from the Solomon Islands and the New Hebrides drew attention to the range of size variation exhibited by specimens referred to this species over its then total range to the Philippine Islands. At that time, the collections of the British Museum (Natural History) contained only the holotype of *M. tristis* sensu stricto, BM(NH) 55.12.26.266, and from New Guinea there were specimens available from no more than two widely separated localities. In view of the paucity of material this author left unresolved the questions posed by the range of variation, except to associate *robustior* Revilliod, 1914 from the Loyalty Islands with *tristis* as a distinct species rather than with *M. australis* as a subspecies as it was described and had been considered hitherto in the literature. Since then two widely divergent views of the classification of this group of bats have emerged which although in agreement in accepting *M. robustior* as a distinct species divide bats formerly regarded as *M. tristis* in different ways. Each of these treatments is based to a considerable extent on the collections of the British Museum (Natural History).

Peterson (1981*b*) recognised *M. tristis* in the Philippine Islands (*M. t. tristis* (Waterhouse, 1845)) and Sulawesi (*M. t. celebensis* Peterson, 1981*b*), with a second species, *M. propitristis,* from western New Guinea (*M. p. grandis* Peterson, 1981*b*), eastern New Guinea (*M. p. propitristis* Peterson, 1981*b*) and from the Bismarck Archipelago, the Solomon Islands and the New Hebrides (*M. p. insularis* Peterson, 1981*b*). This author had available a good series of specimens from the Philippines and based his conclusions in part on a multivariate analysis of a number of characters. Particular morphological features indicated as separating *propitristis* from *tristis* include a greater degree of development of the sagittal crest over the rear of the cranium, lower, flatter rostral profile, greater constriction, or less inflation, of the posterior part of the braincase, a less conspicuous bulging of the supraoccipital (not the supraorbital as stated by Peterson, p. 833) behind the lambdoidal crests, and a wider palate in relation to the length of the toothrow.

Some of these features are not always especially effective in diagnosis. The sagittal crest, for example is little different in the Sulawesian specimens (*tristis*) recorded here than in some of those (*propitristis*) from western New Guinea, while the rostrum of some specimens from western New Guinea is more steeply elevated as in Sulawesian specimens. The constriction of the posterior part of the braincase varies slightly in New Guinea specimens and in a number is little different from those from Sulawesi and although the posterior bulge of the supraoccipital is more conspicuous in Philippine and Sulawesian specimens than in those from western New Guinea, this condition is approached or equalled by others from the eastern part of that island. As Peterson (fig. 7) shows, the width of the rear palate in relation to the length of the toothrow provides a relatively useful diagnostic character, with little overlap between specimens referred to *tristis* and those referred to *propitristis*. However, the Sulawesian population seems equally referable on this feature to *propitristis* as to *tristis*: indeed, with the addition of the specimens recorded here it could be regarded as corresponding quite as closely to the *propitristis* grouping as it does to the Philippine examples.

Maeda (1982), on the other hand, regarded the Philippine population and those from both western and eastern New Guinea and that on New Britain as referable to one species, *M. tristis,* without subspecific separation. He removed the populations on the Solomon Islands and the New Hebrides to a distinct species, *M. melanesiensis,* which he described as new on account of its smaller size, the same grounds as those used by Peterson (1981*b*) in dividing *M. propitristis insularis* from the New Guinea form *M. p. propitristis,* a feature also noted by Hill (1971*a*). Maeda indicated in a footnote (p. 47) that *melanesiensis* is synonymous with *M. p. insularis,* the paper by Peterson being unavailable when his study was in preparation.

Of these treatments that by Peterson (1981*b*) seems the more satisfactory. Maeda (1982) examined only a single Philippine specimen and none from Sulawesi: it is apparent from the tabulated measurements of Hill (1971*a*) and Peterson (1981*b*) that a good case can be made for clinal variation among the populations from eastern New Guinea to the New Hebrides, and both of these authors considered them conspecific. At the same time, their separation from the Sulawesian and Philippine populations as a distinct species seems less strongly based than Peterson (1981) implies. The morphological characters that he cites are not wholly satisfactory and while they may be diagnostic between populations are not always so when these populations are grouped in the way that Peterson suggested. Although in palatal shape the two proposed species seem more definitely separable, there are indications that the Sulawesian population may not fully conform to the criteria set by Peterson for *tristis.* The representation remains small or limited in some instances: the Sulawesian population is known from no more than four specimens, that from western New Guinea from one locality only, and the population in eastern New Guinea only from three locations. Moreover, Koopman (1982) considered only one species involved after examining the characters used by Peterson in relation to specimens in the American Museum of Natural History. In these circumstances I too prefer to regard all as subspecies of *M. tristis,* i.e. *M. t. tristis* (Philippine Islands), *M. t. celebensis* (Sulawesi), *M. t. grandis* (W New Guinea), *M. t. propitristis* (E New Guinea) and *M. t. insularis* (with synonym *M. melanesiensis* Maeda, 1982 from San Christobal Island, Solomon Islands) (Bismarck Archipelago to the New Hebrides).

Miniopterus tristis insularis Peterson, 1981

Miniopterus propitristis insularis Peterson, 1981*b* : 838. Kagilakulaku Cave, Hutuna, Rennell Island, Solomon Islands 11° 45′ S, 160° 15′ E.
Miniopterus melanesiensis Maeda, 1982 : 19. St. (=San) Christobal Island, Solomon Islands.

SPECIMENS EXAMINED. New Hebrides: 3 ♂♂, 3 ♀♀ BM(NH) 73.1547–1552 Hog Harbour, Espiritu Santo I, 150 ft (in alcohol, BM(NH) 73.1548, 73.1552 without skulls; coll. Earl of Cranbrook, Royal Society Expedition to the New Hebrides, 1971).

REMARKS. Specimens from Hog Harbour reported by Baker & Bird (1936) as *M. schreibersii* were referred to *M. tristis* by Hill (1971*a*), this taxon being later divided (above) by Peterson (1981*b*). Others from St. Matthias Island in the Bismarck Archipelago were referred to *insularis* by Peterson (1981*b*) but to *M. oceanensis* (=*M. schreibersii oceanensis* as here understood) by Maeda (1982). Further examination establishes them as belonging to *insularis.*

DISCUSSION. Maeda (1982) has described *Miniopterus bismarckensis* from Manus I, Bismarck Archipelago as a new species in the *tristis* group, basing it on a series of five specimens (BM(NH) 14.4.1.11, 11*–14) in the collections of the British Museum (Natural History). The series appears as population 62 of Maeda (pp. 112, 130): although not noted as such by this author, two (BM(NH) 14.4.1.12,14) are not fully adult. I am unable to agree with Maeda that the length of the tibia in this series measures 16·5–17·5 (p. 112): in the two young examples the tibia measures 17·4 and 16·9 respectively, in the three adults 19·0 (BM(NH) 14.4.1.11.11), 18·7 (BM(NH) 14.4.1.11*) and 18·8 (BM(NH) 14.4.1.13). Forearm lengths in these adults are 46·4, 45·0 and 44·4 respectively. Moreover, I fail totally to understand whence Maeda obtained the total length for five skulls for this form (p. 130). The three adults consist of the rostrum and mandible only, the whole of the cranium beyond the frontal region missing. In BM(NH) 14.4.1.14 the basal part of the cranium and its posteriormost part except the occiput is lost and the best value that can be obtained for total length is 15·1 while in BM(NH) 14.4.1.12 the braincase has been damaged but the rear of the cranium survives. It is thus the only more or less complete example but even so the premaxillae have been damaged and the best value that can be obtained for total length is 16·3. It is difficult to reconcile these facts with Maeda's published value for total length of skull of 15·8–17·3 with a mean of 16·84 in the five examples. Other relevant values for BM(NH) 14.4.1.12 are condylobasal length 16·1, condylocanine length 15·6, least interorbital width 3·6, width of braincase 8·0, mastoid width 8·8 (these last two taken by eyepiece micrometer, the first of these by extrapolation, one side of cranium damaged), m^3–m^3 c. 7·1 (left m^3 missing), c–m^3 7·0, c–m_3 7·3. Of the remaining specimens BM(NH) 14.4.1.11 has lost both rear upper molars and cannot be used for palatal measurements, BM(NH) 14.4.1.11* (the holotype of *bismarckensis*) has the left upper molar displaced but the distance m^3–m^3 can be determined, while BM(NH) 14.4.1.13 is palatally and dentally complete. Such palatal and dental measurements as can be obtained appear in Table 13.

Although Maeda placed *bismarckensis* in the *tristis* group, the dimensions of the one admittedly slightly young skull (BM(NH) 14.4.1.12) that provides enough measurements to satisfy the requirements of his key take this specimen quite emphatically not to the *tristis* group, but to the *fuliginosus, blepotis* or *schreibersii* groups, among which it then keys to the *magnater* subgroup, fitting best with *magnater* or *macrodens* but perfectly with neither. Peterson (1981*b*) also apparently allocated four of these five specimens to *M. propitristis insularis* (=*M. tristis insularis* as understood here) but they are small for this form as he defines it, a point confirmed by a specimen (BM(NH) 39.1407) from New Britain that undoubtedly represents *insularis* and also by a long series of *insularis* from New Ireland that I have been able to examine through the courtesy of Professor James D. Smith of California State University at Fullerton, California. In these the greatest length of skull varied from 17·3–18·0 in 38 examples, the condylobasal length from 16·7–17·5 in 40 specimens, m^3–m^3 from 7·3–8·1 in 40 examples, and c–m^3 from 7·1–7·6 in forty-one. Moreover, the values for m^3–m^3 and c–m^3 that can be established for the specimens from Manus fall considerably outside the limits of *M. t. insularis* in the scatter diagram (p. 836, fig. 7) provided by Peterson, although it appears that he has failed to plot the lowest values given for this form in Table 5 (p. 839). In the relative width of the palate to the length of the toothrow the specimens from Manus agree equally well with *M. magnater magnater* or *M. magnater macrodens.* So far as can be determined the sagittal crest in the specimens from Manus is low rather than well developed as in *insularis,* and the rostrum is less broadened than in that form. While it is difficult to be definitive with such limited material, I am not convinced that these specimens should be referred to the *tristis* group: it is possible that they represent a form allied to *M. magnater.* The point can only be resolved by further, complete specimens from Manus.

MURININAE

Murina suilla (Temminck, 1840)

Vespertilio suillus Temminck, 1840 : 224. Java.

SPECIMENS EXAMINED. Borneo: ♂ BM(NH) 82.548 Samusan Wildlife Sanctuary, between Cape Datu and Gunong Pueh, W Sarawak, c. 1° 55′–2° 00′ N, 109° 34′–109° 39′ E (in alcohol; coll. N. A. MacKenzie); ♂ BM(NH) 82.555 Path to South Hitam, Gomantong, Sabah (in alcohol; coll. C. M. Francis).

REMARKS. The few earlier records of *M. suilla* from Borneo are summarized by Medway (1965, 1977). Length of forearm (BM(NH) 82.548, 82.555) 31·4, 29·2.

Murina aurata Milne Edwards, 1872

Murina aurata Milne Edwards, 1872 : 250, pl. 37b, fig. 1, pl. 37c, fig. 2. Moupin, Szechwan, China.
(?) *Harpiocephalus feae* Thomas, 1891 : 884; 1892 : 926–927. Biapo, Karen Hills, Burma.

SPECIMENS EXAMINED. Nepal: ♂ BM(NH) 75.301 2 km E of Mukut, N of Dhaulagirui, 28° 50′ N, 83° 25′ E, 13,500 ft (skin, skull; coll. G. B. Corbet).

Thailand: ♂ BM(NH) 82.162 Doi Ithanon, Chom Thong, Chiangmai, c. 2550 m, 18° 35′ N, 98° 29′ E (in alcohol, skull extracted; coll. D. S. Melville).

REMARKS. These specimens agree closely with the detailed account of *M. aurata* by Maeda (1980) who also examined and listed BM(NH) 75.301. The species has not before been recorded from Thailand; it may be readily recognised by its small size (length of forearm (7) 28·5–32·0, condylobasal length (6) 12·3–13·1, c–m^3 (7) 4·3–4·6; values in part from Maeda, 1980) and distinctive coloration, the dorsal pelage basally brownish, the hairs with bright, lustrous yellow brown tips, the ventral surface blackish, overlaid with white or greyish white tipping. The upper surface of the forearm and thumb is sparsely covered with brown hairs and the dorsal surface of the uropatagium, the tibiae and feet with a moderate cover of longer, brownish or chestnut hairs. Externally it is very similar to *M. aenea* Hill, 1964 from Malaya but this species has a longer forearm (length (2) 33·7–35·0) and a much larger skull (condylobasal length (2) 15·2–15·9, c–m^3 (2) 5·8–5·9) that is nearer in size to that of *M. cyclotis* Dobson, 1872*b* and has bronze tipped pelage.

DISCUSSION. Ellerman & Morrison-Scott (1951) listed *feae* (Thomas, 1891) as a subspecies of *M. aurata* while Maeda (1980) tentatively synonymised the two but did not examine the holotype of *feae*, which is probably in the Museo Civico di Storia Naturale Giacomo Doria in Genoa. Certainly from the description *feae* is very like *aurata,* differing chiefly in the absence of any distinct fringe of hairs along the edge of the uropatagium and in its duller, more brownish coloration. Moreover, the holotype did not come from northern Burma as Maeda indicated, but from the Carin or Karen Hills, northeast of Toungoo, in the more southerly part of the country. Indeed, this location is not greatly distant from Doi Ithanon, whence *aurata* is here recorded. In the restricted sense of Maeda (1980) who excluded specimens from northeastern Asia and Japan as a distinct species only twelve examples (including the holotype of *feae*) of *M. aurata* have been reported, their range extending through the montane parts of northern India, Nepal, Burma and Thailand to Szechuan and Yunnan.

Murina tubinaris (Scully, 1881)

Harpiocephalus tubinaris Scully, 1881 : 200, fig. 1. Gilgit, Kashmir.

Specimen examined. Thailand: ♂ BM(NH) 82.163 Doi Inthanon, Chom Thong, Chiangmai, c. 1650 m, 18° 35′ N, 98° 29′ E (in alcohol, skull extracted; coll. D. S. Melville).

Remarks. This is the first of *M. tubinaris* to be reported from Thailand. It agrees closely with specimens of this species from northeastern India and northern Burma and is greyish brown dorsally and greyish white ventrally, the upper surface of the forearms, tail, legs and uropatagium sparsely or only moderately clothed with greyish brown hairs. The anterior premolars (pm$\frac{2}{2}$) are considerably reduced to one half or less than one half the crown area of the second premolars (pm$\frac{4}{4}$) and to about two thirds of their height. The species differs from *M. cyclotis* and from *M. huttonii* (Peters, 1872*a*) in its chiefly greyish and not brownish dorsal colour, in more convergent upper toothrows, more reduced anterior premolars and in less massive molar teeth. Although similar in length of forearm to *M. aurata* it has a slightly larger skull (length of forearm (19) 29·0–32·0; condylobasal length (12) 13·3–14·2, c–m^3 (15) 4·8–5·2).

Discussion. Hill (1962) recorded *M. tubinaris* from northern Burma, considering it a species distinct from *M. huttonii* with which it had been associated as a subspecies by Ellerman & Morrison-Scott (1951), the same author later (1964) describing and discussing it in more detail. Its discovery in the northern part of Thailand is not unexpected: it occurs otherwise from Kashmir through northern India and Burma apparently to Vietnam.

Murina cyclotis cyclotis Dobson, 1872

Murina cyclotis Dobson, 1872*b* : 210; 1873*c* : 206. Darjeeling, northeastern India.

Specimens examined. Thailand: ♂ BM(NH) 82.164 Doi Inthanon, Chom Thong, Chiangmai, c. 1650 m, 18° 35′ N, 98° 29′ E (in alcohol); ♂ BM(NH) 82.165 Doi Pha Hom Pok, c. 1650 m (in alcohol, skull extracted; both coll. D. S. Melville).

Remarks. As with the earlier example of *M. cyclotis* reported from Chiangmai by Hill & Thonglongya (1972) these specimens agree closely with the definition of the species by Hill (1964) and with examples in the British Museum (Natural History) from Burma. Dorsally *M. cyclotis* is generally some shade of rufous brown or ferrugineous, the ventral surface predominantly greyish white: the forearms, tail, tibiae, feet and uropatagium have a dense clothing of short, golden brown hairs on the upper surface. Young specimens are darker and browner. Coloration apart, the nominate subspecies is larger cranially (length of forearm (9) 30·2–34·8, condylobasal length (8) 14·7–15·8, c–m^3 (9) 5·0–5·7) than either *M. aurata* or *M. tubinaris*: a yet larger subspecies *M. c. peninsularis* Hill, 1964 occurs in the Malay Peninsula and in Borneo (vide infra) (length of forearm (9) 33·7–38·8, condylobasal length (9) 15·4–16·9, c–m^3 (9) 5·5–6·2). Dentally, *M. cyclotis* may be distinguished by the lack of reduction of the anterior upper premolar (pm^2) which in crown area is equal to three quarters or more of the crown area of the second upper premolar (pm^4), and by the reduction of the posterior triangles or talonids of its molar teeth, the paracones and protocones of the first (m^1) and second (m^2) upper molars being slightly reduced, the hypoconids and entoconids of the corresponding lower teeth very much more so, sometimes scarcely evident, and separated from the protoconids and metaconids only by a very narrow trough.

Discussion. Four species of *Murina* have now been reported from Thailand, namely *M. aurata, M. tubinaris, M. cyclotis* and *M. huttonii* (Peters, 1872*a*), the last being reported from Chiangmai by Hill (1975) and Lekagul & McNeely (1977). This rather larger (length of forearm (11) 33·2–37·0, condylobasal length (10) 15·3–16·7, c–m^3 (11) 5·8–6·1) species is more brownish than *M. tubinaris* and like *M. cyclotis* does not have markedly convergent upper toothrows. The anterior upper premolar (pm^2) is a little more reduced than in the latter species, the tooth one half to two thirds the crown area of the second upper premolar (pm^4), while the hypoconids and entoconids of the first and second (m$_{1-2}$) lower molars are well developed and separated from the protoconids and metaconids by a comparatively wide trough.

Murina cyclotis peninsularis Hill, 1964

Murina cyclotis peninsularis Hill, 1964: 55. Ulu Chemperoh, near Janda Baik, Bentong District, Pahang, Malaya, c. 3° 18′ N, 101° 50′ E, 2000 ft.

SPECIMENS EXAMINED. Borneo: ♂ BM(NH) 78.1543 Melinau R, Gunung Mulu National Park, Sarawak (in alcohol, skull extracted; coll. D. R. Wells, Royal Geographical Society Expedition to Gunung Mulu, ♂ BM(NH) 82.556 Sepilok Forest Reserve, Sabah (in alcohol, skull extracted; coll: C. M. Francis).

REMARKS. Only *M. suilla* among tube-nosed bats has been reported until now from Borneo, *M. cyclotis* being known hitherto from the mainland of southeastern Asia and from single specimens from the islands of Hainan off southeastern China and Mindanao in the Philippine Islands. These Bornean specimens agree closely with *M. c. peninsularis* from Malaya, to which they are referred.

Measurements (BM(NH) 78.1543, 82.556), with those of seven Malayan examples in parentheses: length of forearm 37·0, 35·6 (33·7–38·8); greatest length of skull 18·8, 18·4 (17·4–18·9); condylobasal length 16·9, 16·8 (15·4–16·7); length orbit–gnathion 4·6, 4·5 (4·2–4·5); palatal length 9·3, 9·2 (8·2–9·3); rostral width at lachrymals 6·3, 6·3 (5·5–6·0); least interorbital width 4·3, 4·5 (4·3–4·6); zygomatic width 11·3, 10·9 (9·9–10·9); width of braincase 8·3, 8·3 (7·7–8·2); height of braincase 7·1, 6·8 (6·6–6·9); mastoid width 9·4, 9·2 (8·3–9·1); c^1–c^1 (cingula) 5·3, 5·2 (4·5–5·2), (alveoli) 5·1, 5·1 (4·5–5·1); m^3–m^3 6·1, 6·0 (5·6–6·0); c–m^3 6·1, 6·0 (5·5–6·2); length complete mandible from condyles 12·3, 12·0 (10·9–12·1); length right ramus from condyle 12·8, 12·5 (11·2–12·7); c–m_3 6·4, 6·2 (6·0–6·4).

DISCUSSION. There exist now apparently nine known examples of this large subspecies: in addition to those recorded here from Borneo and those reported from Malaya by Hill (1964, 1972) the collections of the British Museum (Natural History) also include two further specimens from Malaya, BM(NH) 73.630–631, both male, from Telok Chempedak, Pahang.

Murina sp.

SPECIMEN EXAMINED. Molucca Islands: ♀ BM(NH) 82.144 (juv.) Latuhalat, Amboina I (in alcohol; coll. B. H. Gaskell, 'Operation Drake').

REMARKS. It is not possible to attempt any further identification of this juvenile example in which the milk dentition is not yet completely lost and the adult dentition only partially erupted.

DISCUSSION. Records of tube-nosed bats of the genus *Murina* from the region east of Borneo are few (Van Deusen, 1961). The genus has yet to be reported from Sulawesi itself, although it has been recorded from the nearby island of Peleng by Tate (1941*e*): it is also known from the Lesser Sunda Islands (Flores, Sumbawa), from the Moluccas (Ceram, Buru, Goram), New Guinea and the Bismarck Archipelago (Ruk (=Umboi) I). According to Van Deusen (1961) the specimens forming the basis of these records total fourteen: more recently, Richards (1981) and Richards *et al.* (1982) have reported a further example of the genus from Queensland, Australia. The specimen recorded here is the first of *Murina* to be recorded from Amboina, where clearly it might be expected to occur.

Three taxa have been named from the region: *florium* Thomas, 1908*b* from Flores, *lanosa* Thomas, 1910*b* from Ceram, and *toxopei* (=*toxopeusi*) Thomas, 1923 from Buru. Laurie & Hill (1954) considered *lanosa* and *toxopeusi* conspecific with *florium,* regarding specimens from Sumbawa originally recorded by Mertens (1936) as *M. suilla* more probably representative of *M. f. florium.* Tate (1941*e*) found the specimens from Peleng Island conformed closely to *M. florium,* while Hill (in Van Deusen, 1961) thought the example from Ruk I, originally recorded by Thomas (1914*a*) without specific identification, to be close to *toxopeusi.* Van Deusen (1961) considered that an evaluation of the characters on which these taxa were based seemed to indicate that only one good species existed east of Wallace's Line, but through lack of comparative material did not attempt to apply a specific name to the specimen that he recorded from New Guinea. Richards *et al.* (1982) referred the specimen from Queensland to *M. florium.*

A further examination of the limited material in the collection of the British Museum (Natural History) supports the view that only one species is involved, *florium, lanosa* and *toxopeusi* being almost certainly conspecific. All are larger, especially cranially, than *M. suilla* from Java and its closely related congeners *balstoni* Thomas, 1908*b,* also from Java, and *canescens* Thomas, 1923*a,* from Nias Island, off the west coast of Sumatra, both very similar to *suilla* and possibly no more than subspecifically different from it. Only the holotypes of *florium* (BM(NH)63.12.26.14) and *toxopeusi* (BM(NH)23.1.2.27) are available, with the holotype (BM(NH) 10.3.4.24) and one other example (BM(NH) 7.1.1.482) of *lanosa* from Ceram, together with a specimen (BM(NH) 10.3.4.115) from Goram referred to *lanosa* by Laurie & Hill (1954) and the specimen (BM(NH) 14.4.1.33) recorded from Ruk Island by Thomas (1914*a*). Removal of the skull from the specimen from Goram confirms that it represents *lanosa* rather than *toxopeusi.* The example from Ruk, however, has a shallow median

Table 14 Measurements of *Murina* from east of Wallace's Line.

	M. florium florium Holotype BM(NH) 63.12.26.14 Flores I	*M. florium lanosa* Holotype ♀ BM(NH) 10.3.4.24 Ceram I	*M. florium lanosa* BM(NH) 7.1.1.482 Ceram I	*M. florium lanosa* BM(NH) 10.3.4.115 Goram I	*M. florium toxopeusi* Holotype ♂ BM(NH) 23.1.2.27 Buru I	*M. ? florium* ♀ BM(NH) 14.4.1.33 Ruk I, Bismarck Is	*M. ? florium* Van Deusen (1961) New Guinea	*M. florium* Richards *et al.* (1982) Queensland, Australia
Length of forearm	34·8	36·9	36·4	36·9	34·4	35·4	35	35·7
Greatest length of skull	—	16·7	—	17·3	16·7	—	15·4	16·9
Condylobasal length	—	15·5	—	15·7	15·3	—		15·8
Condylocanine length	—	14·8	—	15·1	14·7	—		
Palatal length	—	7·2	—	7·0	7·1	—		
Width across anteorbital foramina	4·5	4·3	4·5	4·5	4·2	4·3		
Least interorbital width	4·2	4·5	4·3	4·5	4·2	4·4	4·3	4·6
Zygomatic width	—	9·2	—	9·5	9·3	—	8·9	10·2
Width of braincase	—	7·9	—	7·9	7·6	—	7·8	8·1
Mastoid width	—	8·2	—	8·4	8·0	—		
c^1–c^1 (alveoli)	3·8	3·9	4·0	4·0	3·8	4·0		
m^3–m^3	5·6	5·4	5·6	5·6	5·5	5·7		6·1
c–m^3	5·3	5·5	5·6	5·6	5·5	5·6	5·3	5·8
Length complete mandible from condyles	10·8	11·3	11·1	11·2	11·0	11·3		
Length right ramus from condyle	11·1	11·4	11·6	11·5	11·4	11·6		
c–m_3	6·0	6·1	6·2	6·2	6·1	6·3		6·2

rostral sulcus and its anterior upper premolar (pm^2) is longitudinally compressed and rather short, in these respects agreeing more closely with the holotype of *toxopeusi* than with *lanosa*. Although the Goram specimen has a slightly shallower sulcus than the examples of *lanosa* from Ceram, its pm^2 is less compressed than in the specimen from Ruk. These specimens, with the exception of the skull of the specimen from Goram, were first examined in 1961 at the instigation of the late Mr H. M. van Deusen of the American Museum of Natural History.

KERIVOULINAE

Kerivoula hardwickei hardwickei (Horsfield, 1824)

Vespertilio hardwickii Horsfield, 1824 (unpaginated). Java.

SPECIMENS EXAMINED. C Sulawesi: ♂♂ BM(NH) 82.145–146 R Ranu, 1° 51′ S, 121° 30′ E (in alcohol, skulls extracted; coll. B. H. Gaskell, 'Operation Drake').

REMARKS. The larger (BM(NH) 82.146) of these examples tends in some respects to bridge the slight disparity in certain elements of size noted by Hill (1965) between specimens of *K. h. hardwickei* from more easterly localities (Philippine Islands, Borneo and Sulawesi) and those from more westerly locations (Java, Sumatra and Malaya). Measurements (BM(NH) 82.145, 82.146): length of forearm 31·7, 33·1; greatest length of skull 12·7, 13·6; condylobasal length 12·3, 12·9; condylocanine length 11·9, 12·6; least interorbital width 3·1, 3·3; zygomatic width 7·7, 8·0; width of braincase 6·7, 6·7; depth of braincase 5·5, 5·7; mastoid width 7·0, 7·3; c^1–c^1 (alveoli) 3·3, 3·3; m^3–m^3 4·9, 5·2; c–m^3 5·1, 5·4; length complete mandible from condyle 9·0, 9·6; length right ramus from condyle 9·2, 9·8; c–m^3 5·4, 5·7.

Kerivoula papillosa (?) malayana Chasen, 1940

Kerivoula papillosa malayana Chasen, 1940 : 55. Ginting Bedai, Selangor–Pahang boundary, Malaya, 2300 ft.

SPECIMEN EXAMINED. C Sulawesi: ♂ BM(NH) 82.147 R Ranu, 1° 51′ S, 121° 30′ E (in alcohol, skull extracted; coll. B. H. Gaskell, 'Operation Drake').

REMARKS. This is the first of *K. papillosa* to be recorded from Sulawesi, the species being known hitherto from northeastern India to Sumatra, Borneo and Java. It agrees closely with *K. p. malayana*, reported hitherto as far east as Borneo. The collections of the British Museum (Natural History) do not include specimens of *K. p. papillosa* (Temminck, 1840) from Java: according to Tate (1941*e*), Bornean specimens agree in all essential respects with the type from Java but Chasen (1940) remarked that the few skins that he had seen from Java were rather greyer than those that he referred to *malayana*, with which he included Bornean examples. Chasen noted further that the skulls of Javan specimens are smaller than those of Malayan and Bornean examples, with a maximum length of about 17 but Tate gives measurements of a 'cotype' in the Rijksmuseum van Natuurlijke Historie, Leiden that suggest that this may not be so.

Measurements of the Sulawesian specimen: length of forearm 44·9; greatest length of skull 18·0; condylobasal length 16·5; condylocanine length 16·4; least interorbital width 3·6; zygomatic width 11·5; width of braincase 8·4; depth of braincase 7·3; mastoid width 9·1; c^1–c^1 (alveoli) 4·6; width inside m^1–m^1 3·1; m^3–m^3 6·6; c–m^3 7·4; m^{1-3} 3·9; length complete mandible from condyle 12·6; length right ramus from condyle 13·0, c–m_3 7·9.

Kerivoula muscina Tate, 1941

Kerivoula muscina Tate, 1941*e* : 586. Lake Daviumbu, 6 miles above mouth of Strickland R, middle Fly R, Western Division, Papua, c. 20 m.

Specimen examined. Papua New Guinea: ♂ BM(NH) 80.668 Buso, Morobe, 7° 17′ S, 147° 08′ E (in alcohol, skull extracted; coll. B. H. Gaskell, 'Operation Drake').

Remarks. In size, cranial architecture and dentition this specimen agrees closely with the descriptions of *K. muscina* by Tate (1941*e*) and Hill (1965). Measurements: length of forearm 33·0; greatest length of skull 13·5; condylobasal length —; condylocanine length —; least interorbital width 3·2; zygomatic width —; width of braincase 6·8; mastoid width 7·2; c^1–c^1 (alveoli) 3·2; m^3–m^3 5·0; width palato-pterygoid extension 1·7; width of cochleae 2·4; width apart of cochleae 1·3; c–m^3 5·5; m^{1-3} 2·7; length complete mandible from condyles 9·8; length right ramus from condyle 10·0; c–m_3 5·9.

MOLOSSIDAE

Tadarida (Chaerephon) plicata (Buchannan, 1800)

Vespertilio plicatus Buchanan, 1800 : 261, pl. 13. Bengal.

Specimens examined. Sex indet. BM(NH) 78.2509 Lubang Rusa, Gunong Mulu National Park, 4th Division, Sarawak (mummified, skull; coll. Earl of Cranbrook, Royal Geographical Society Expedition to Mount Mulu); 2♂♂, ♀ (all yg.) BM(NH) 931–933 Mouth of Deer Cave, Gunung Mulu National Park (in alcohol; coll. C. H. Fry, Royal Geographical Society Expedition to Mount Mulu); 4 ♂♂ (3 yg.), 2 ♀♀ (1. yg.) BM(NH) 956–961 Deer Cave (in alcohol; coll. P. Chapman, Royal Society Expedition to Mount Mulu); ♂, ♀ BM(NH) 79.1400–1401 Deer Cave (in alcohol; coll. S. Proctor, Royal Society Expedition to Mount Mulu); sex indet. BM(NH) 79.953–954 Madai Cave, Sabah (skeletal parts); ♂ Sabah Museum No. NH 95 Madai Cave (in alcohol) (all from Sabah Museum).

Remarks. There are relatively few published records of *T. plicata* from Borneo. The species has been reported previously from Pengkalan Forest, 1st Division in Sarawak by Medway (1965) and in Sabah from Madai by Chasen (1931), Gomanton by Pryer (1884) and from Sapagaya by Davis (1962). Length of forearm in 6 adults 40·4–43·5.

Discussion. Specimens from Borneo are usually referred to *T. p. plicata* (Hill, 1961*b*; Medway, 1965). As Davis (1962) pointed out, however, the forearm in Bornean specimens averages shorter than in those from Java (?*T. p. dilatata* Horsfield, 1822) and is also shorter on the average than in the nominate subspecies. In forearm length they approach the Philippine form *T. p. luzonus* Hollister, 1913 or the more doubtful *T. p. tenuis* (Horfield, 1822) from eastern Java, recognised by Chasen (1940), Tate (1941*c*) and Hill (1961*b*).

Tadarida (Chaerephon) jobensis jobensis (Miller, 1902)

Nyctinomus jobensis Miller, 1902 : 246. Ansus, Jobi I, Geelvinck Bay, West Irian.

Specimens examined. Papua New Guinea: 9 ♂♂, 14 ♀♀BM(NH) 80.669–679, 80.681–692 Buso, Morobe, 7° 17′ S, 147° 08′ E (in alcohol; coll. B. H. Gaskell, 'Operation Drake').

Remarks. These specimens with length of forearm (23) 43·3–47·9 confirm that in *T. j. jobensis* the forearm is rather shorter than in *T. j. colonicus* (Thomas, 1906*a*) from northern Australia which has a forearm length of (6) 47·0–52·2, but is generally longer than in *T. j. solomonis* (Troughton, 1931) from the Solomon Islands, for which the describer gave a forearm length of (200) 40·5–45.

Tadarida (Chaerephon) jobensis bregullae Felten, 1964

Tadarida jobensis bregullae Felten, 1964 : 9. Malo I, New Hebrides.

Specimens examined. New Hebrides: ♀, ♂ BM(NH) 73.1553–1534 Tan Lensingo Cave, Abounatori Village, Malo I, 30 m; ♂♂ BM(NH) 73.1555–1568 Abounatori Village, 30 m (BM(NH) 73.1553–1566 in alcohol, 73.1567–1568 skins, skulls; obtained by the Earl of Cranbrook, Royal Society Expedition to the New Hebrides, 1971).

Remarks. These are the first of *T. j. bregullae* to be reported since the subspecies was described. The length of the forearm in 15 fully adult examples ranges from 47·6–51·4, rather more widely than in the ten of the original specimens measured and reported by Felten. In forearm length the subspecies is similar to *T. j. colonicus* but according to the describer has a narrower skull, a contention supported by skulls from the present series.

Cranial measurements of BM(NH) 73.1567, 73.1568 with (in parentheses) those of 8 of *colonicus,* from Felten, (1964) who also included measurements made by Hill (1961*b*); condylobasal length 18·5, 18·4 (18·3–19·7); least interorbital width 4·1, 4·0 (4·0–4·4); zygomatic width 11·8, 11·4 (11·9–13·1); width of braincase 9·5, 9·3 (9·5–10·4); mastoid width 10·8, 10·7 (11·1–11·9); c^1–c^1 (alveoli) 5·4, 5·2 (5·2–6·1); m^3–m^3 (alveoli) 8·5, 8·3 (8·9–9·5); c–m^3 (crowns) 7·5, 7·5 (—), (alveoli) 7·2, 7·2 (7·3–7·7).

Discussion. Freeman (1981) synonymised *T. j. bregullae* but whether into *T. j. jobensis, T. j. colonicus* or *T. j. solomonis* is not clear. Its various dimensional differences from these, however, suggest that at least for the present it should be retained.

Tadarida (Mormopterus) beccarii astrolabiensis (Meyer, 1899)

Nyctinomus astrolabiensis Meyer, 1899 : 19, pl. 10, figs. 19, 30, pl. 11, fig. 6. Bongu, Astrolabe Bay, West Irian.

Specimens examined. Papua New Guinea: ♀♀ BM(NH) 80.680, 80.693, 80.695 Buso, Morobe, 7° 17′ S, 147° 08′ E (in alcohol, skulls of BM(NH) 80.693, 80.695 extracted; coll. B. H. Gaskell, 'Operation Drake').

Australia: ♀ BM(NH) 78.2708 Mount Wando, 36 miles SSW of Emerald, C Queensland, 23° 56′ S, 147° 46′ E (coll. G. Gordon & B. C. Lawrie); ♂ BM(NH) 78.2709 Barret's Lagoon, NE Queensland, 18° 03′ S, 145° 58′ E (coll. R. J. Grimes) (both in alcohol, skulls extracted; from F. R. Allison, through National Parks and Wildlife Service).

Remarks. Relatively few specimens of *T. b. astrolabiensis* have been recorded: these agree closely with a small series (BM(NH) 11.11.11.18–20) in the British Museum (Natural History) from the Mimika River, West Irian. The nominate subspecies *T. b. beccarii* (Peters, 1881) from Amboina Island is represented in London by no more than three examples (BM(NH) 10.7.25.17–19) and has a slightly shorter and in some respects slightly narrower skull with a shorter toothrow than *T. b. astrolabiensis.*

Measurements of specimens from New Guinea, including the Mimika River series (BM(NH) 11.11.11.18–20) first measured by Hill (1961*b*), with (in parentheses) corresponding values for *T. b. beccarii* from Amboina (BM(NH) 10.7.25.17–19 in that order, skulls BM(NH) 10.7.25.18–19): length of forearm (6) 33·3–35·9 (33·4, 34·3, 34·9); greatest length of skull (5) 17·3–18·3 (16·6, 16·6); condylobasal length (5) 16·5–17·3 (16·0, 16·1); condylocanine length (5) 16·2–16·9 (15·7, 15·7); least interorbital width (5) 4·2–4·7 (4·2, 4·2); zygomatic width (2) 11·0, 11·7 (—, —); width of braincase (5) 8·0–8·5 (8·0, 8·1); mastoid width (5) 10·3–10·8 (9·7, —); c^1–c^1 (alveoli) (5) 4·5–5·0 (4·6, 4·2); m^3–m^3 (alveoli) (5) 7·7–8·2 (7·5, 7·3); c–m^3 (crowns) (5) 6·4–6·6 (5·9, 6·0), (alveoli) (5) 6·2–6·4 (5·8, 5·9); pm^4–m^3 (alveoli) (5) 4·7–4·9 (4·5, 4·6); length complete mandible from condyles (4) 11·9–12·6 (11·2, 11·5); length right ramus from condyle (4) 12·6–13·0 (11·7, 12·0); c–m_3 (crowns) (4) 6·8–7·0 (6·4, 6·4).

The species does not appear to have been formally reported hitherto from Queensland or indeed from Australia but F. R. Allison in Honacki *et al.* (1982) includes N Australia within its distribution. The two specimens reported here are nearer in size to *T. b. astrolabiensis* than to the nominate subspecies but have longer forearms and slightly more massive canine teeth. It seems possible that adequate series of specimens might permit the recognition of an Australian subspecies. Measurements BM(NH) 78.2708, 78.2709): length of forearm 37·9, 36·4; greatest length of skull 17·1, 18·1; condylobasal length 16·9, 17·9; condylocanine length 16·1, 17·1; least interorbital width 4·0, 4·5; zygomatic width —, —; width of braincase 8·2, 8·6; mastoid width —, 10·9; c^1–c^1 (alveoli) 6·2, 6·5; m^3–m^3 (alveoli) 7·3, 8·2; c–m^3 (crowns) 6·4, 6·7, (alveoli) 6·2, 6·5; pm^4–m^3 (alveoli) 4·8, 5·1; length of complete mandible from condyles 12·1, 12·9; length right ramus from condyle 12·8, 13·5; c–m_3 (crowns) 6·8, 7·2.

The small anterior upper premolar (pm^2) is absent from the left side of the jaw but present in the other side in BM(NH) 80.693, the opposite condition occurring in BM(NH) 80.695, while in BM(NH) 80.680 it is absent from both sides: it is present in both sides in the Australian examples. The absence of this tooth from one of the Amboina specimens (*T. b. beccarii*) and from two of those from the Mimika River (*T. b. astrolabiensis*) was noted by Hill (1961*b*).

Discussion. Freeman (1981) raised *Mormopterus* to generic rank. Certainly it is one of the most distinctive of the subgenera of *Tadarida*, its relatively delicate, angular ears of thin integument, with small antitragal lobe, and its finely wrinkled upper lip setting it apart from the other subgenera.

Tadarida sp.

Specimen examined. Papua New Guinea: Sex indet. BM(NH) 80.696 (nurseling). Buso, Morobe, 7° 17′ S, 147° 08′ E (in alcohol; coll. B. H. Gaskell, 'Operation Drake').

Otomops papuensis Lawrence, 1948

Otomops papuensis Lawrence, 1948 : 413. Vailala R (flows into Gulf of Papua about 15 miles W of Kerema).

Specimens examined. Papua New Guinea: ♂♀ BM(NH) 73.136–137 Maul, Mount Suckling, 300 m (BM(NH) 73.136 skin, skull, 73.137 in alcohol; coll. J. I. Menzies).

Remarks. These appear to be the first of *O. papuensis* to be reported since its description: they conform closely to the original account. The dorsal surface is reddish brown, the hairs slightly paler at the base, the overall colour a little darker on the crown, the lower back and along the junction of the wings with the body. There is a band of paler, light brown hairs across the shoulders. The ventral surface is a paler reddish brown than the back, with a diffuse, slightly paler area across the base of the throat. The skull is as it is described by Lawrence but the male skull examined has a low sagittal crest that extends posteriorly to join slight lambdoidal ridges. As Lawrence points out, these project forward in an anteriorly directed V-shape to leave the rear of the skull smoothly rounded.

External measurements (BM(NH) 73.136, 73.137): length of forearm 49·6, 50·2; cranial measurements (BM(NH) 73.136): greatest length of skull 19·6; condylobasal length 17·9; condylocanine length 17·2; basal length 16·1; length from posterior edge of narial aperture to highest point of cranium 14·7; least interorbital width 4·3; zygomatic width 10·4; width of braincase 9·4; mastoid width 10·6; bottom of bulla to highest point of braincase 9·7; height of jugal projection of zygoma 2·1; c^1–c^1 (alveoli) 4·2; m^3–m^3 (alveoli) 7·9; i^2–m^3 8·2; c–m^3 7·2;

length complete mandible from condyles 12·2; length right ramus from condyle 12·5; c–m_3 7·5.

Discussion. Two species of *Otomops* occur in New Guinea: the other, *O. secundus* Hayman, 1952, known so far from Tapu, Upper Ramu River Plateau, Papua New Guinea, differs from *O. papuensis* chiefly in its longer forearm (length 57–58), dark chocolate brown general coloration, the presence of a broad, well-defined buffy grey mantle and of a narrow but conspicuous line of white hairs along the dorsal surface of the endopatagium at its junction with the body. There is also a patch of white hairs at the anterior part of the inner or medial base of each ear, flanking the interaural pocket, a point unremarked by Hayman in the original account. A similar patch of hairs occurs in *O. wroughtoni* (Thomas, 1913) from India but the base of the outer margin of the ear in *O. secundus* lacks the sprinkling of white hairs found in this species. There is no white at the base of the ear in *O. papuensis,* the hairs instead a rich reddish brown with slightly paler bases. *Otomops secundus* seems in fact nearer in external size and coloration to *O. formosus* Chasen, 1939 from Java or to the larger *O. wroughtoni.* The representation of all except *O. wroughtoni* is small: all have skulls essentially similar in structure, while the skull of *O. secundus* is closely similar in size to that of *O. papuensis.*

Summary

In the Megachiroptera *Rousettus amplexicaudatus stresemanni* from New Guinea is considered a valid subspecies; further material of the Sulawesian species *Rousettus celebensis, Styloctenium wallacei* and *Thoopterus nigrescens* is reported and where appropriate discussed; a number of species of *Dobsonia* are reviewed; Indo-Australian *Cynopterus* are examined in detail and *C. titthaecheileus* considered specifically distinct; Javan *Chironax melanocephalus* is re-described and further examples are reported from Sumatra and Sulawesi; a series of *Harpyionycteris celebensis* is reported and discussed; *Nyctimene celaeno* is provisionally considered specifically distinct; *Eonycteris* in Indo-Australia is briefly reviewed and the nomenclature of *Macroglossus* re-examined; *Synconcyteris* is reviewed and further specimens of *Notopteris macdonaldi macdonaldi* are reported and discussed.

Among the Microchiroptera *Rhinolophus celebensis* and *R. borneensis* are considered distinct species and their subspecies allocated with *R. importunus* considered a subspecies of the latter. The Sulawesian *Hipposideros dinops pelingensis* and *H. inexpectatus* are compared. Indo-Australian *Myotis* have been examined in some detail with a review of *M. muricola* and *M. mystacinus*; *M. ater* is considered a distinct species and the status of *M. australis* Dobson, 1878 discussed; the large-footed species *M. horsfieldii, M. hasseltii* and *M. adversus* are reviewed and keyed and a new subspecies, *M. adversus orientis* is described from the New Hebrides. Certain Indo-Australian *Pipistrellus* are briefly reviewed, notably *P. tenuis,* and the second known specimen of *P. societatis* is reported. A new species of *Hesperoptenus, H. gaskelli,* is described from Sulawesi. Indo-Australian *Miniopterus* are reviewed in detail and recent revisionary work on this part of the genus is discussed with a number of proposed changes in its classification: *M. solomonensis* Maeda, 1982 is considered a subspecies of *M. australis*; *M. macrocneme* Revilliod, 1914 a subspecies of *M. pusillus*; *M. oceanensis* Maeda, 1982 a subspecies of *M. schreibersii*; *M. macrodens* Maeda, 1982 a subspecies of *M. magnater*; *M. propitristis* Peterson, 1981 conspecific with *M. tristis*; the status of *M. bismarckensis* Maeda, 1982 is discussed. Occurrences of *Murina* east of Wallace's Line are examined and further specimens of *Tadarida (Chaerephon) jobensis bregullae* and *Otomops papuensis* are reported.

The following new records and range extensions are reported in this paper: *Dobsonia viridis (?) viridis* from Sulawesi; *Cynopterus brachyotis brachyotis* from Burma and *C. titthaecheileus* and *Macroglossus sobrinus sobrinus* from Krakatoa I; *Megaerops (?) ecaudatus from* northeastern India; *Aethalops alecto* from Java; *Taphozous melanopogon* from Sulawesi; *Megaderma spasma niasense* from Siberut I; *Rhinolophus pusillus pusillus, Hipposideros ridleyi* and *Coelops robinsoni* from Borneo; *Myotis muricola (?) browni* from Sulawesi; *M. ater* from Siberut I, *M. hasseltii continentis* from Burma; *Pipistrellus vordermanni* from Borneo; *Miniopterus australis tibialis* from Sulawesi, *M. pusillus* and *M. magnater macrodens* from Sumatra; *Murina suilla* and *M. tubinaris* from Thailand, *M. cyclotis peninsularis* from Borneo; *Kerivoula papillosa (?) malayana* from Sulawesi and *Tadarida (Mormopterus) beccarii* from Australia.

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Addendum

While this paper was in press a further contribution by Maeda *et al.* (1982) became available in London. On the basis of specimens from Sabah these authors considered *magnater* a distinct species and suggested that the specimens in the British Museum (Natural History) from Hong Kong (BM(NH) 65.1017 (sic), Pahang (BM(NH) 67.217) and Upper Burma (BM(NH) 32.11.1.3) might represent it. They also suggested that the forearm lengths given by Lekagul & McNeely (1977) for *schreibersii* in Thailand and by Medway (1978) in Malaya indicated that specimens referable to *magnater* might have been included. This study clearly antedates the more detailed work by Maeda (1982).

Maeda K., Harada, M. & Kobayashi, T. 1982. Roost observations of *Miniopterus* in Madai Cave, Sabah, East Malaysia. *Zool. Mag. Tokyo* **91** : 125–134, 5 figs.

British Museum (Natural History)
An Atlas of Freshwater Testate Amoebae
C. G. Ogden & R. H. Hedley

1980, Hardcovers, 222pp, £17.50 (£18.00 by post). Co-published by British Museum (Natural History) and Oxford University Press.

This book illustrates, using scanning electron micrographs, most of the common species of testate amoebae that are found in freshwater habitats. Information on the biology, ecology, geographical distribution and a classification are followed by descriptions of ninety-five species. Each of these is illustrated by several views of the shell.

The text is designed not only to enable biologists to identify species of testate amoebae, but to serve as an introduction to students interested in the taxonomy and biology of these freshwater protozoa. It will be of special interest to protozoologists, ecologists, limnologists, water treatment specialists and micropalaeontologists interested in recent sediments.

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On *Macropleurodus, Chilotilapia* (Teleostei, Cichlidae), and the interrelationships of African cichlid species flocks

Peter Humphry Greenwood

Zoology series Vol 45 No 4 25 August 1983

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On *Macropleurodus*, *Chilotilapia* (Teleostei, Cichlidae), and the interrelationships of African cichlid species flocks

Peter Humphry Greenwood
Department of Zoology, British Museum (Natural History), Cromwell Road, London SW7 5HD

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Synopsis

The monotypic cichlid genera *Macropleurodus bicolor* from Lake Victoria, and *Chilotilapia rhoadesi* from Lake Malawi share an outstandingly derived dentition of a kind not recorded in any other members of the family.

Since both taxa share, uniquely, such a derived character complex, it might be thought that they also share a recent common ancestry not shared with other members of the Lake Malawi and Lake Tanganyika cichlid species flocks. A detailed consideration of other anatomical and morphological features indicates that the dental similarity is a homoplastic feature. However, it seems probable that both taxa are members of a monophyletic lineage within the haplochromine cichlids, and that representatives of this lineage occur in Lakes Malawi, Victoria and Tanganyika.

The features previously used to establish the monophyly of the Lake Malawi haplochromine species are found to be unsuitable for that purpose. Other characters suggest, on the contrary, that the species flocks of Lakes Victoria, Malawi and Tanganyika are each composed of several distinct lineages, and that members of at least some lineages occur in more than one lake.

Introduction

Little attention has been given to the problem of interrelating the endemic cichlid faunas of the major African lakes, Tanganyika, Malawi and Victoria (but see Stiassny, 1981). In part this lack of enquiry can be attributed to the size of the problem, over 500 species are involved, in part to a long established idea that the African cichlids can be separated into haplochromine and tilapiine lineages, hence some similarities were simply ascribed to convergent evolution, and in part to another long standing assumption, that within a lake all the taxa in either lineage are most closely related to one another (hence the greater concern with intra- rather than interlake relationships; Regan, 1920, 1922*a* & *b*; Trewavas, 1935 & 1949; Fryer & Iles, 1972; Greenwood, 1974).

Recent investigations have cast considerable doubt on the concept of a simple

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haplochromine–tilapiine dichotomy in the phylogeny of African cichlids (see discussions in Fryer & Iles, 1972, and Greenwood, 1978). This changed viewpoint has, in a sense, complicated the issue. Lake Tanganyika species once thought to be tilapiine stock and therefore convergent mimics of haplochromine taxa in Lake Malawi (see Regan, 1922*a*: 675; Fryer & Iles, 1972: 513–8) must now have their phyletic relationships reassessed. Such reassessment also involves species from Lake Victoria because convergence has been invoked to explain similarities between certain species of that lake with others from Malawi and Tanganyika (Regan, 1922*b*: 159). Further complications arise from evidence which suggests that the postulated monophyly of the haplochromine and the tilapiine species in each lake is questionable (Greenwood, 1980), a suggestion which also questions the previously assumed close relationships of the endemic species in a particular lake.

In short, the whole problem of phyletic interrelationships needs critical reexamination in the light of information gathered since Regan's and Trewavas' pioneering researches on these fishes. It also requires, because different levels of relationship are involved, that the search for sister-taxa be extended beyond the confines of a single lake, a possibility that was not critically examined in the past. Then, as more recently (Regan, 1920; 1922*a* & *b*; Trewavas, 1935; 1949; Greenwood, 1974), the tendency has been to identify anatomically generalized 'ancestral' species for each lake fauna, rather than to search for congruent and uniquely shared derived features, synapomorphies, which might indicate common descent irrespective of a taxon's present geographical locality.

On reflection, it would seem that previous surveys have too readily invoked 'convergence' and 'parallelism' to explain similarity between members of different lake faunas, and that the assumptions were made without hard evidence based on critical analysis. Likewise, the mono- or at most, oligophyletic origin of a particular lake's fauna, or elements of its fauna when 'haplochromine' and 'tilapiine' lineages are involved, have also been assumed without sufficient evidence.

Unfortunately, the large number of species involved, coupled with the very disparate levels of information available on the anatomy and ontogeny of those species, requires that a piecemeal approach to the problems be adopted. The limitations and pitfalls of such an approach are serious. But, considering the size of the problem and the need to overhaul the bases for previous and sometimes inhibiting assumptions, even a piecemeal approach can be profitable.

This present paper centres around two monotypic genera, *Chilotilapia rhoadesi* Blgr., 1908, from Lake Malawi, and *Macropleurodus bicolor* (Blgr) 1906, from Lake Victoria.

Both share a very characteristic dental pattern and tooth form neither of which is found in any other cichlids, either African or American (see Figs 1–10). Ontogenetically, too, they are alike in the way the dental pattern develops, and in having a dental succession involving at least two, and probably three distinct types of teeth. Not surprisingly, larger individuals in both taxa have similar feeding habits. Both crush molluscs between massive jaw teeth before ingesting the soft parts of their prey (Fryer & Iles, 1972; Greenwood, 1956; 1974).

Intergeneric similarities extend beyond these dental and trophic features, although some are certainly correlates. The resemblances include marked similarity in the morphology of the jaws, the syncranial architecture, and in certain myological details.

The two species would almost certainly be placed in single genus if they occurred in the same lake basin. Thus, there would seem to be an *a priori* case for considering the genera to be closely related.

The ranking of *Chilotilapia* and *Macropleurodus* as distinct and not particularly closely related genera has been influenced by three major considerations. First, the belief that the haplochromine species of any one lake are more closely related to one another than to species from other lakes (Regan, 1922*b*: 165). Second, the idea that, in Lake Malawi, this relationship is manifest in certain marker characters carried by most of its endemic haplochromines including *Chilotilapia* (Regan, 1922*b*: 158; Trewavas, 1949), and thirdly, a misunderstanding by some workers (Trewavas, 1935: 68; see also Fryer & Iles, 1974: 75) about the fundamental nature of the definitive tooth form in *Chilotilapia*.

Regan (1922*b*: 159) did, however, notice a basic similarity in the dental morphology and pattern of *Macropleurodus* and *Chilotilapia*. But, since he considered the cichlids of Lakes Victoria and Malawi to be but distantly related, and the two taxa to be members of different lineages, it was inevitable that he should attribute their similarities to convergent evolution.

Trewavas (1935: 69–70), on the other hand, recognized that *Chilotilapia* was in fact a member of Regan's haplochromine group, as is *Macropleurodus*, but made no comments on the close similarity of its dentition with that of *Macropleurodus*. Because of its peculiar dentition in relation to that of other endemic Malawi haplochromines, Trewavas maintained the generic status of *Chilotilapia* and suggested on other characters (*op. cit*: 110), that its nearest living relative was a species in that lake, *Haplochromis euchilus* (see p. 222 *et seq.*).

Before considering these different viewpoints and the whole question of relationships, if any, between the cichlids of Lakes Victoria, Malawi and Tanganyika, detailed comments must be made on the dentition and other anatomical features of both *Chilotilapia* and *Macropleurodus*.

Materials and abbreviations

The entire British Museum (Nat. Hist.) collection of cichlid dry skeletal material and alizarin transparencies used in previous studies on the interrelationships of African haplochromines, was utilized in the preparation of this paper (see Greenwood, 1980; 1983).

Additional dry skeletons were made from:
Macropleurodus bicolor: 1955.2.10:3; 1955.2.10:63–64; 1955.2.10:74–79 two preparations.
Chilotilapia rhoadesi: 1935.6.14: 2121–6; 1935.6.14:2103–2112 three preparations.

Dissections on the jaw and branchial muscles were made on:
Macropleurodus bicolor: 1955.2.10:74–79 three specimens.
Chilotilapia rhoadesi: 1935.6.14:2121–6, and 1935.6.14:2102–2112.
Additional but partial dissections were also made on specimens from this lot.

Dissections of the branchial musculature only were made from:
Astatotilapia burtoni: 1950.4.1:2176–2200
Aulonocranus dewindti: 1960.9.30:4629–4641
Grammatotria lemairei: 1930.4.1:3758–3785

Dissections of the jaw muscles were made on:
Ptyochromis annectens: 1956.10.9:84–87

The use of the letters M, T, or V in parentheses after a generic or specific name indicates the taxon is from, respectively, Lake Malawi, Tanganyika or Victoria. For the purposes of this paper, the haplochromine fauna of Lake Victoria is taken to include that of Lakes Edward and George, Kioga, and Kivu since several of the genera discussed occur in, but only in, all five lakes (see Greenwood, 1980).

All abbreviations used in text figures are amplified in the relevant figure captions.

Dental characters, and their ontogeny, in *Chilotilapia rhoadesi* and *Macropleurodus bicolor*

The definitive, and most characteristic, dentition of *Chilotilapia* (Fig. 3) is apparent only in fishes over 120 mm standard length (SL), but even in smaller fishes the teeth are already distinctive (Fig. 2).

The outer row teeth in both jaws of fishes throughout the size range available, 48–200 mm SL, are mostly stout bicuspids. The minor cusp is small but distinct, the major cusp slightly protracted, the neck nearly cylindrical in cross-section, and the crown somewhat incurved

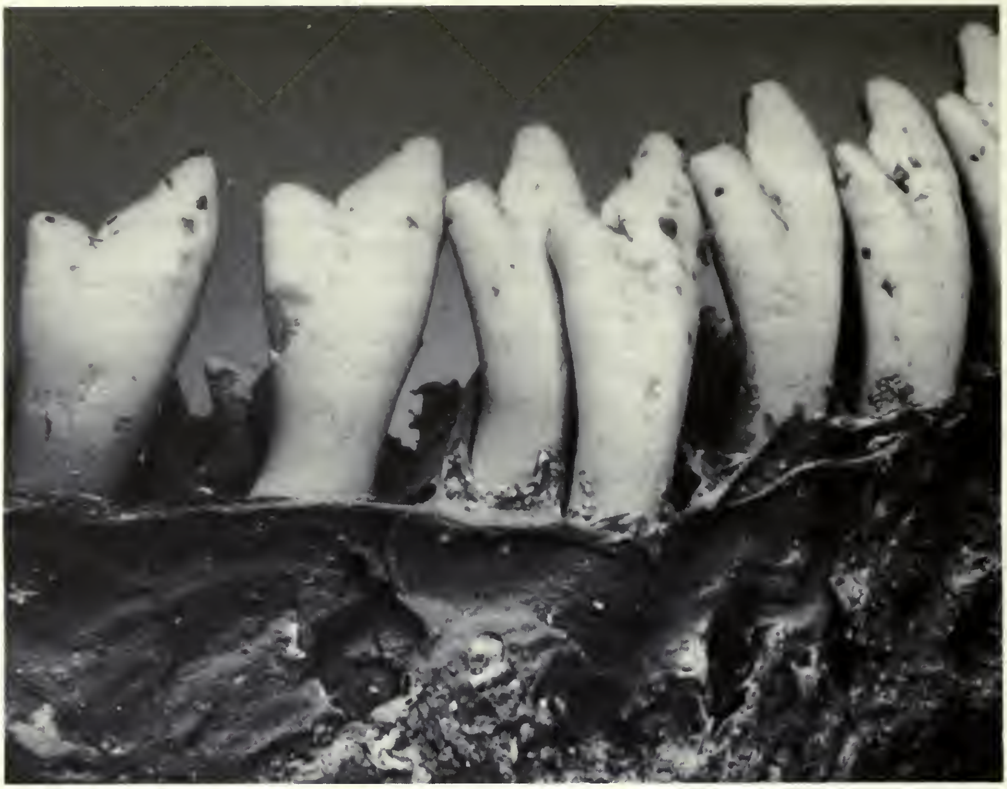

Fig. 1 *Macropleurodus bicolor.* Scanning electron micrograph of anterolateral teeth in the outer row of the left premaxilla, seen in labial view (67·5 × N.S.). From a specimen 58 mm standard length.

buccally (Figs 2 & 6). With increasing body size the teeth gradually become stouter, the crown less compressed except at its extreme occlusal edge, and the minor cusp is reduced further, partly it would seem through wear, but also through its absolute reduction in teeth of successive replacement generations.

A second, and essentially tricuspid, tooth type (Fig. 3) first appears in fishes of between 105 and 115 mm SL. Such teeth sometimes predominate in the outer tooth rows of specimens > 140 mm SL; but even when this is so a number of bicuspids persist and may be the predominant form even in fishes as large as 220 mm SL.

In the tricuspid teeth the major cusp is still clearly the largest one, and has virtually the proportions and shape of that cusp in bicuspids but it is slightly more protracted. The two minor cusps are situated at the base of the major one, i.e. are labial in position, are of equal or subequal size, and unless greatly worn, have their rounded tips at the same level as the occlusal surface of the major cusp. A shallow groove, most marked in unerupted and newly erupted teeth, lies between the minor cusps and extends for a short distance onto the occlusal surface of the major cusp.

It is these teeth which Trewavas (1935:67) described as having '... crowns shaped like a grain of wheat...' I cannot, however, agree with her statement (*loc. cit*) that in adult fishes all the outer teeth are of this kind. Certainly in some large fishes the majority of teeth is of that kind, but in other and even larger specimens tricuspids are poorly represented. Their number generally increases with the size of the fish; none is present in specimens less than 105 mm SL.

As noted before, the essentially tricuspid nature of 'wheat grain' teeth is most obvious in

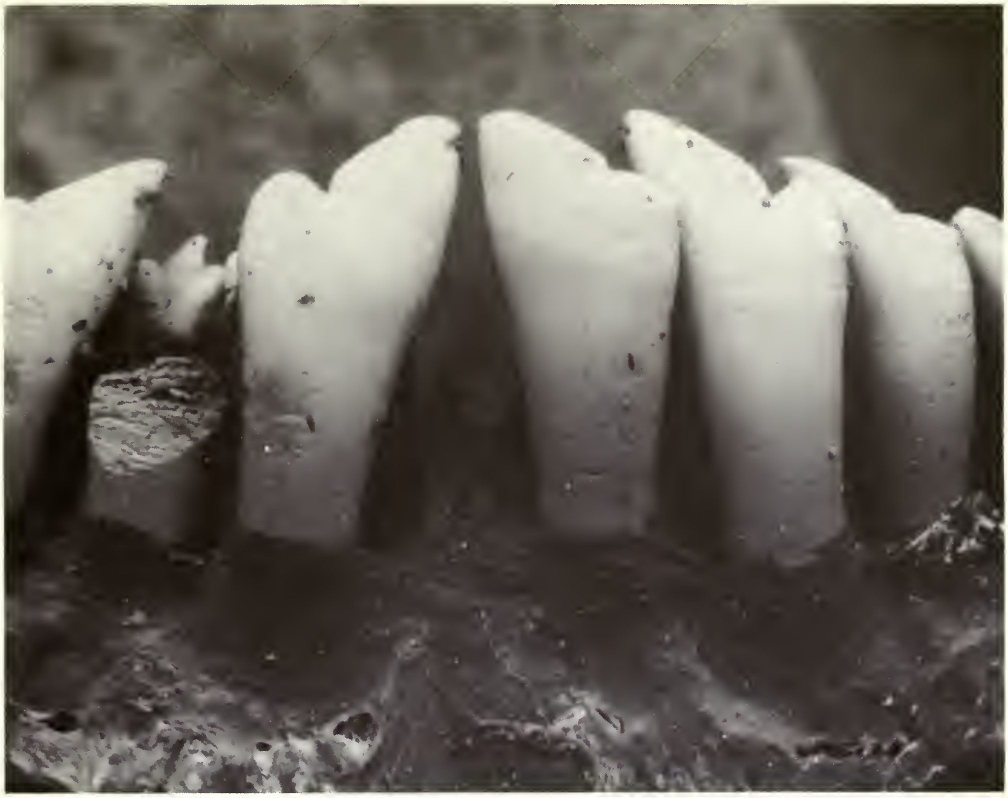

Fig. 2 *Chilotilapia rhoadesi.* Scanning electron micrograph of anterior outer row premaxillary teeth situated on either side of the premaxillary symphysis, seen in labial view (42 × N.S.). From a specimen 65 mm standard length.

newly erupted teeth. With wear the distinctiveness of the minor cusps is lost and the groove between them almost obliterated. The tooth then assumed the appearance of a conical unicuspid in which the crown is aligned almost at right angles to the neck. Since, ontogenetically, predecessors of the tricuspid teeth are bicuspids, and since bicuspids occur together with the 'wheat grain' tricuspids, I cannot agree with Fryer & Iles' (1972:75) description of the dentition in *Chilotilapia* as 'basically conical'.

In addition to size-related changes in tooth form, there are similarly correlated changes in tooth alignment (see Fig. 6).

Most specimens less than 95 mm SL have the outer row teeth of the premaxilla arranged so that the occlusal surface of the major cusp is aligned in parallel with the long axis of the bone, the tips of the crowns following one another in a gently curving arc (Fig. 6). Exceptionally, in some fishes from the upper part of this size range, i.e. 80–90 mm SL, the lateral and posterolateral teeth, rarely only the anterior ones, are implanted so that the crown is angled across the long axis of the bone. The tip of the major cusp points medially, that of the minor one labially.

Specimens of standard lengths greater than 95 mm have the crowns of all teeth in the outer premaxillary row directed medially, but with the anterior teeth less angled than the others (Fig. 6).

Changes in the implantation angle of the outer row teeth in the dentary begin at a smaller body size than do those of the premaxilla. At a standard length of *ca* 70 mm the posterior and posterolateral teeth are distinctly angled, although even at a standard length of 110 mm the crowns of the anterior and anterolateral teeth are but slightly displaced towards the mid-

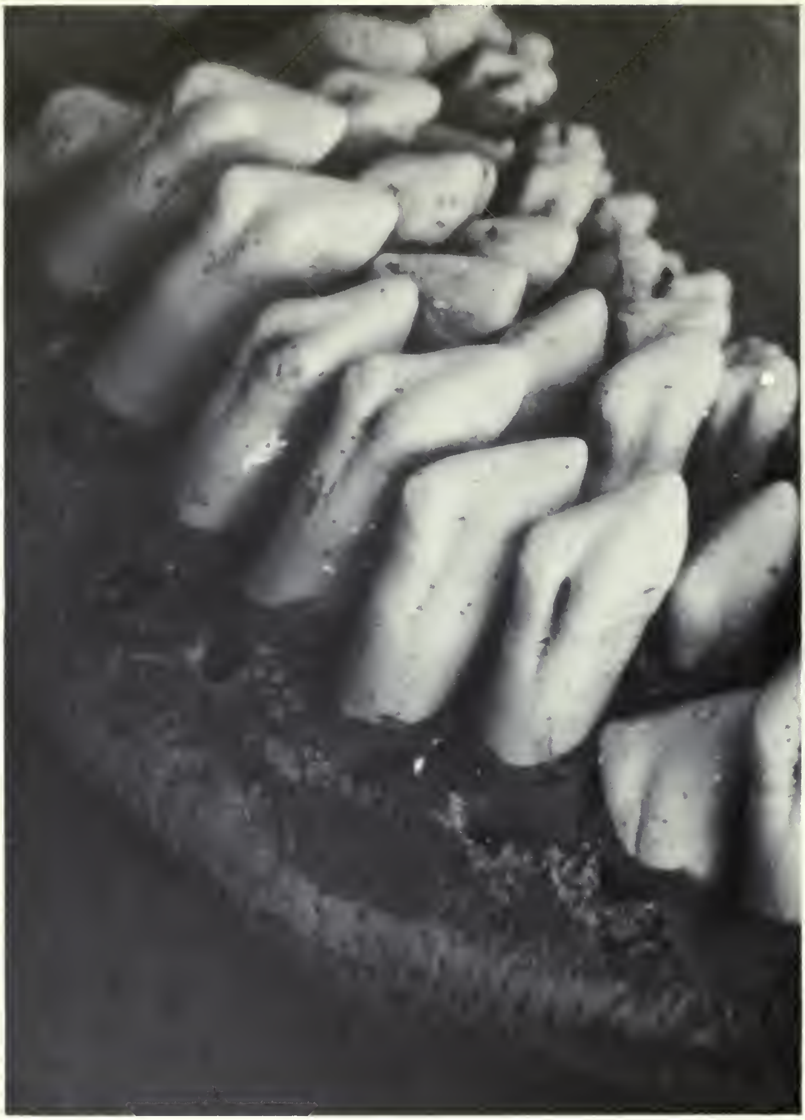

Fig. 3 *Chilotilapia rhoadesi.* Scanning electron micrograph of anterior and anterolateral teeth (outer and some inner rows) of the right premaxilla, seen in oblique and somewhat posterior occlusal view (11·6× N.S.). From a specimen 151 mm standard length.

line. In somewhat larger individuals, however, all the outer teeth on the dentary are distinctly angled, the anterior teeth now directed medially at a greater angle than their counterparts on the premaxilla.

It has not been possible to identify the underlying mechanical causes of these shifts in tooth alignment. That is to say, whether succeeding teeth erupt and are then fused to the bone at a different angle from that of their predecessors, or whether teeth already fixed to the jaw undergo a relative change of angle as a result of differential growth changes in the underlying bone. Certain features suggest, however, that differential bone growth may be responsible. For example, changes in the orientation of individual teeth are coordinate over whole sections of the jaw, yet tooth replacement is irregular and should thus lead to individual teeth

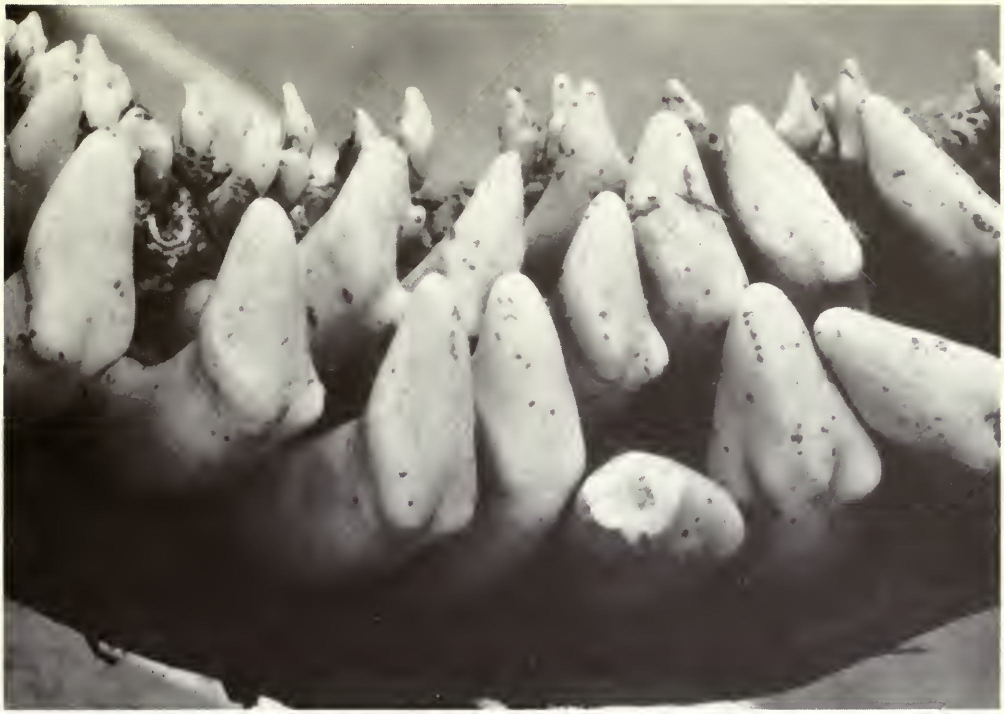

Fig. 4 *Macropleurodus bicolor.* Occlusal surface of anterior and anterolateral outer and inner row teeth from the right premaxilla, seen in oblique and somewhat lateral view (17·0× N.S.). From a specimen 120 mm standard length.

in any one section being at different angles depending on their time of eruption. Also, those areas of the jaw in which the most marked angling occurs are coincident with regions of the bone which undergo the most marked differential growth, that is, expansion and curvature. These regions are the lateral and posterolateral sections of the premaxilla, and the anterior and anterolateral regions of the dentary's alveolar surface.

Teeth forming the inner tooth rows in both jaws also show marked ontogenetic changes in shape and size. The smallest individuals examined, 48–57 mm SL, have mostly small tricuspid teeth in these series, although there are usually a few and slightly larger teeth situated posterolaterally in the premaxilla, where there is but a single inner tooth row. All the inner teeth in fishes of this size group are of the common tricuspid type. That is, with two small lateral cusps flanking a larger central cusp, and the whole crown gently recurved.

Fishes between 60 and 105 mm SL show a gradual replacement of preexisting premaxillary teeth by stouter and coarser ones. Posterolaterally the replacements are bicuspids closely resembling, but smaller than, the teeth of the outer row (see p. 211 above). Elsewhere in the upper jaw the replacements are either stouter versions of the earlier tricuspids, or, more commonly, stout and weakly tricuspid teeth in which the median cusp is so dominant that the tooth is all but unicuspid.

The inner rows of dentary teeth, which are virtually confined to the anterior and anterolateral parts of the bone, undergo similar changes in specimens of the same size ranges. Some 'wheat grain' teeth, smaller versions of those in the outer row, may be present in the outermost series of the inner dentary rows; one exceptional fish has almost the entire outermost row composed of such teeth.

As body growth proceeds beyond about the 100 mm SL mark, so are increasing numbers of inner row premaxillary teeth replaced by bicuspids which, although smaller than those

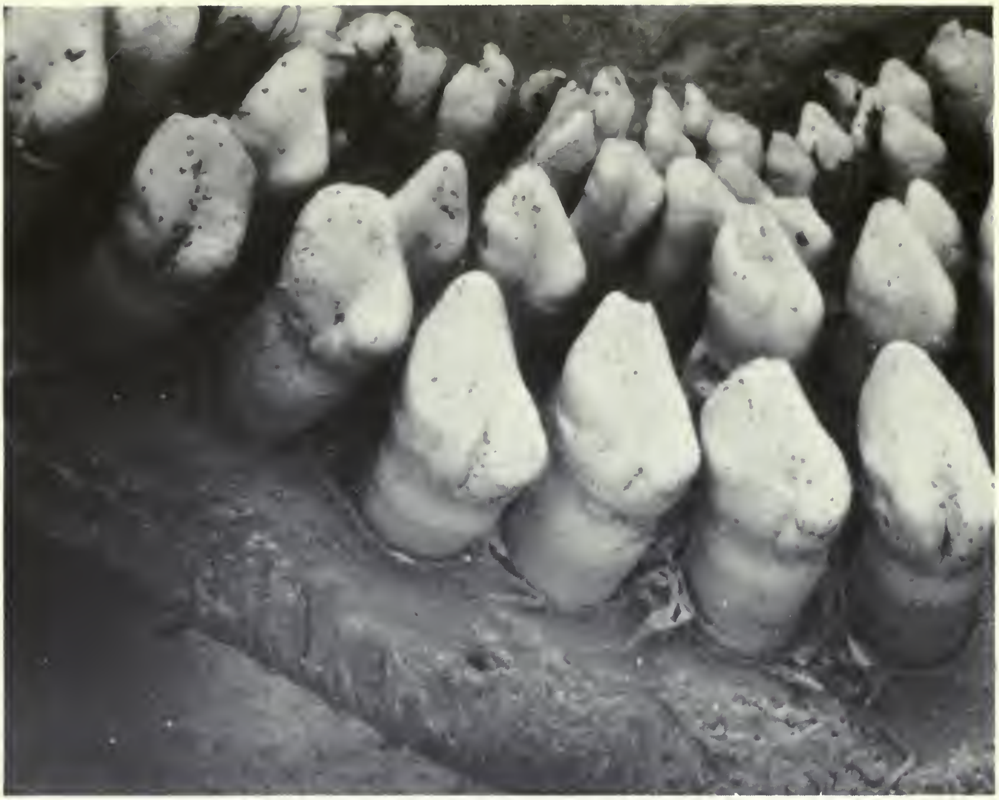

Fig. 5 *Chilotilapia rhoadesi.* Occlusal surface of anterior and anterolateral outer and inner row teeth on the left premaxilla, seen in oblique and somewhat lateral view (12·8× N.S.). From a specimen 190 mm standard length.

of the outer row, closely resemble them in gross morphology. Laterally and posterolaterally a few 'wheat grain' teeth make their first appearance in the inner tooth rows of the premaxilla. Only the innermost one or two rows retain small and weakly tricuspid teeth, or an admixture of these with small unicuspids.

In the largest fishes examined, i.e. 160–220 mm SL, the lateral and posterolateral regions of the premaxilla have at least 2 or 3 rows of noticeably enlarged teeth. These may be of the 'wheat grain' type, bicuspids or an admixture of both types.

Noticeably enlarged inner teeth on the dentary of large fishes are confined to the anterior and anterolateral part of the outermost series. However, all teeth in the succeeding rows, except the innermost one and those in the lateral part of the outermost row, are relatively enlarged. Like all inner teeth on this bone, they are slightly smaller than their counterparts on the premaxilla.

The number of tooth rows in both jaws increases, somewhat irregularly, with increasing body length. The smallest specimen examined, 48 mm SL, has 2, in places 3, rows in both jaws, the largest specimen, 220 mm SL, has 5 rows. Specimens in the middle size range may have 3 or 4 rows in each jaw, that number not always correlated with the fish's length.

At first glance, larger fishes seem to have more teeth laterally and posterolaterally in the premaxilla. This, however, is illusory, a result of the teeth in that region of the bone being slightly larger and less closely arranged than elsewhere. In this region too, there is less space between the tips of the teeth, the interspaces between them being taken up by the enlarged crowns. Thus, this area of the premaxillary occlusal surface is, effectively, more compact than it is elsewhere on the bone.

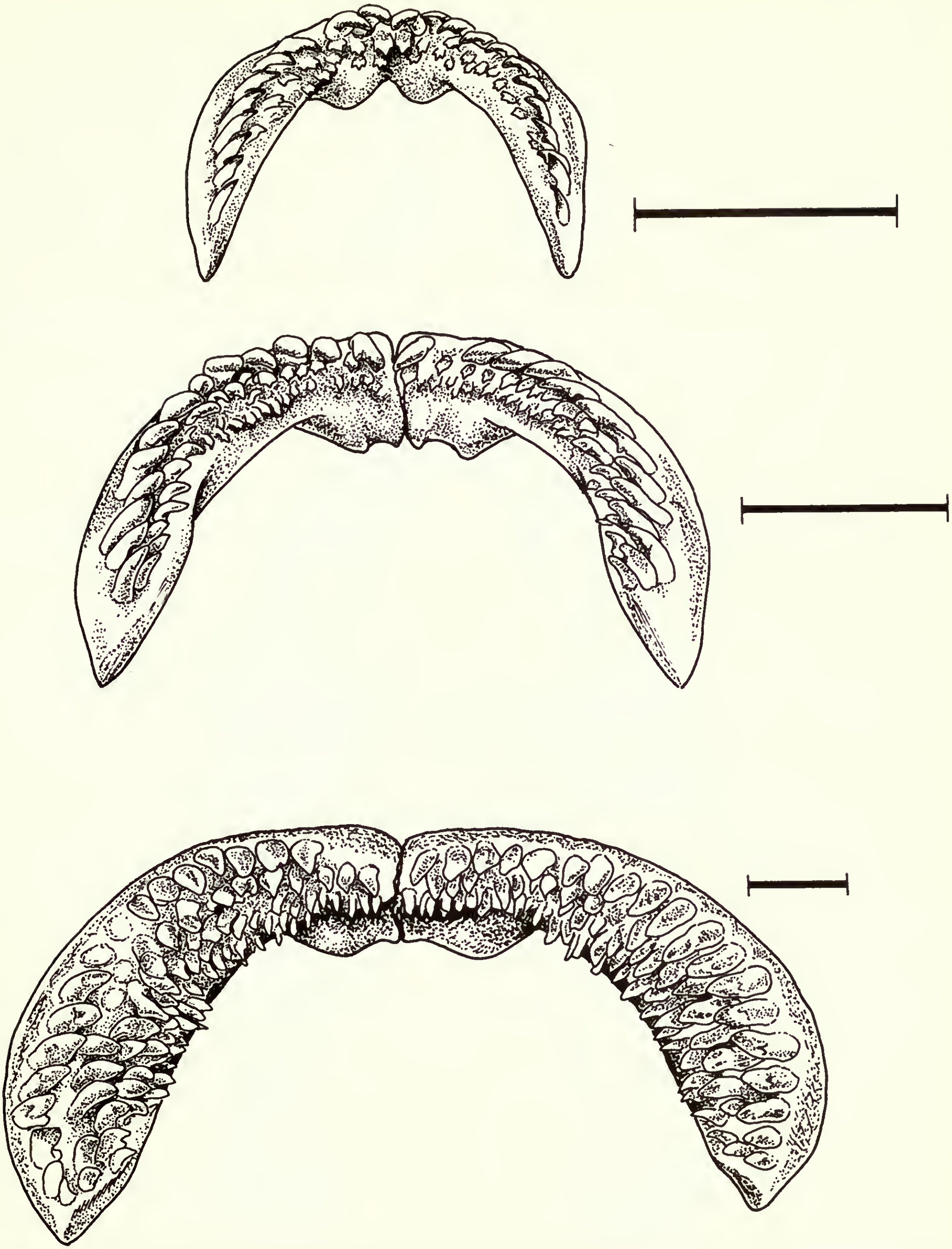

Fig. 6 *Chilotilapia rhoadesi.* Premaxilla showing dentigerous surface in occlusal view; from specimens 65·0 (top) 98·0 and 190·0 mm standard length respectively. Scale = 3 mm.

Tooth number in the outer row of the premaxilla ranges from 20–30 in fishes < 100 mm SL, with fishes in the 48–70 mm range having, in general, 20–24 teeth, and from 24–40 in fishes 105–220 mm SL.

Ontogenetic changes in jaw shape were mentioned earlier (p. 215). These involve, principally, the premaxilla. In the smallest skeleton examined, from a fish 65 mm SL, there is, relative to the generalized condition, an obvious broadening of the premaxilla and its alveolar surface over the lateral and posterolateral extent of the horizontal arms (Fig. 6). This broadening becomes more pronounced with growth, and the widened area extends from its former anterior position to encompass the posterior parts of the arm as well (Fig. 6). Correlated with these changes there is an overall thickening and inflation of the horizontal arms and a change in the outline shape of the entire premaxillary occlusal surface. The latter changes from one which is broadly U-shaped, to one in which the base of the U is flattened and extended laterally (see Fig. 6).

Alterations in the shape and proportions of the dentary are somewhat less pronounced, and involve, mainly, a thickening and outward bulging of the anterior and anterolateral alveolar surfaces and the bone immediately underlying them. There is also a change in occlusal outline correlated with the changing outline of the premaxilla (Fig. 7).

The distinctive dentition, dental pattern and jaw bone morphology characterizing *Chilotilapia* are repeated, with only minor differences, in *Macropleurodus bicolor*, as are their ontogenies (cf. Figs 1, 4, 8 & 9, with 2, 3, 5, 6 & 7).

Departures from the *Chilotilapia* condition occurring in *Macropleurodus* are:

1. The major cusp in all bicuspid outer row teeth, and in the definitive tricuspid 'wheat-grain' teeth, is more protracted than in *Chilotilapia* (cf. Figs 3 & 5 with 4). As in that genus, however, the major cusp becomes relatively stouter and almost cylindrical in the largest teeth.
2. The two minor cusps in a 'wheat-grain' tricuspid are lower than in *Chilotilapia,* and the groove between them is shallower. The minor cusps are often worn away in larger fishes.
3. The widened posterior and posterolateral region of the premaxillary alveolar surface in larger fishes is, relatively speaking, slightly narrower in *Macropleurodus* (cf. Figs 6 & 8).
4. There are fewer inner tooth rows laterally and posterolaterally in the premaxilla of *Macropleurodus*, usually 1 or 2, compared with 2–5 in *Chilotilapia*; the number in that taxon, but not *Macropleurodus,* being partially correlated with the fish's size.
5. One or occasionally both arms of the premaxilla are bowed in the vertical plane (see Greenwood, 1956:306–7; 1980:80–81).
6. The different tooth forms, especially the 'wheat-grain' type, first appear in individuals of a smaller size. However, it should be recalled that individuals of *Chilotilapia* reach a larger maximum adult size, at least 220 mm SL, than do those of *Macropleurodus*, 150 mm SL, modal range 110–130 mm. That *Chilotilapia* has more rows of premaxillary inner teeth (see p. 216) may also be related to the larger adult sizes attained in that genus.

The buccal larvae of *Macropleurodus bicolor,* at a total length of about 9·0 mm, have slender and conical outer teeth in both jaws (Greenwood, 1956: 308). Similar teeth occur in the buccal larvae of *Astatotilapia macrops* at a comparable developmental stage; adults of that species have the generalized bicuspid tooth type found in many haplochromine cichlids (see Greenwood, 1979 & 1980). Unfortunately no larval *Chilotilapia* are available for examination.

Compared with intergeneric dental differences in other cichlids, those distinguishing *Chilotilapia* and *Macropleurodus* are very slight. Indeed, they are of a kind which, on current taxonomic practice, would not be rated at more than 'specific-differences' if the two taxa were sympatric.

From a phylogenetic viewpoint these uniquely shared and derived dental features of *Chilotilapia* and *Macropleurodus* would seem to indicate a recent common ancestry for the two taxa. To test that hypothesis, which contradicts current views on the relationships of the two genera, see p. 211 above, a search was made for characters that might refute it.

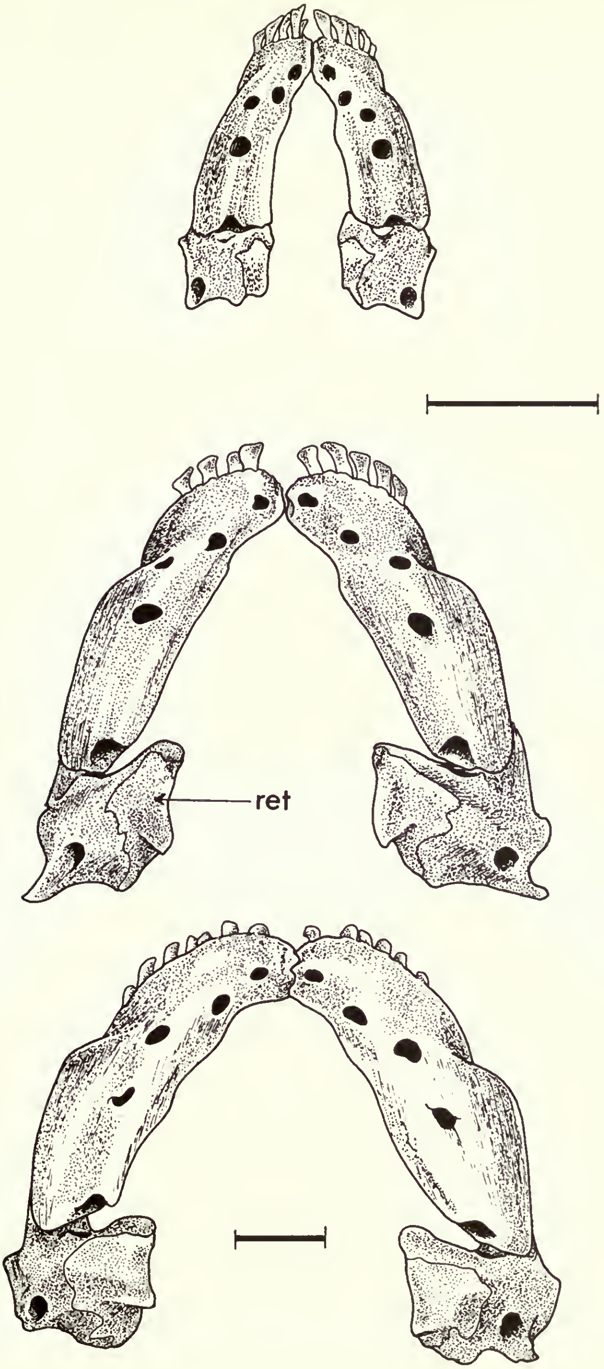

Fig. 7 *Chilotilapia rhoadesi.* Lower jaw in ventral view; from specimens 65·0 (top) 98·0 and 190·0 mm standard length respectively. ret = retroarticular. Scale = 3 mm.

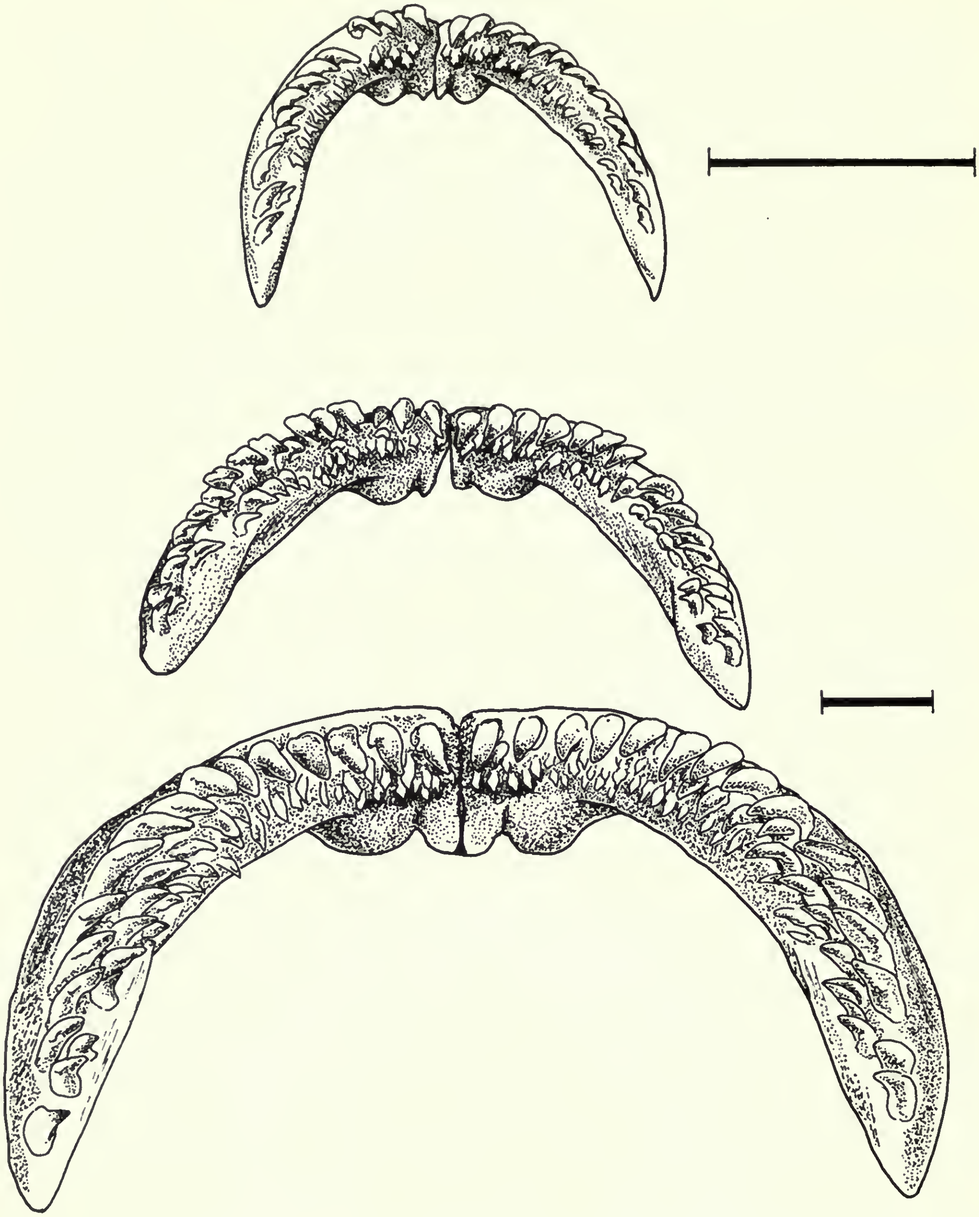

Fig. 8 *Macropleurodus bicolor.* Premaxilla, showing dentigerous surface in occlusal view; from specimens 58·0 (top), 115·0 and 144·0 mm standard length respectively. Scale = 3 mm.

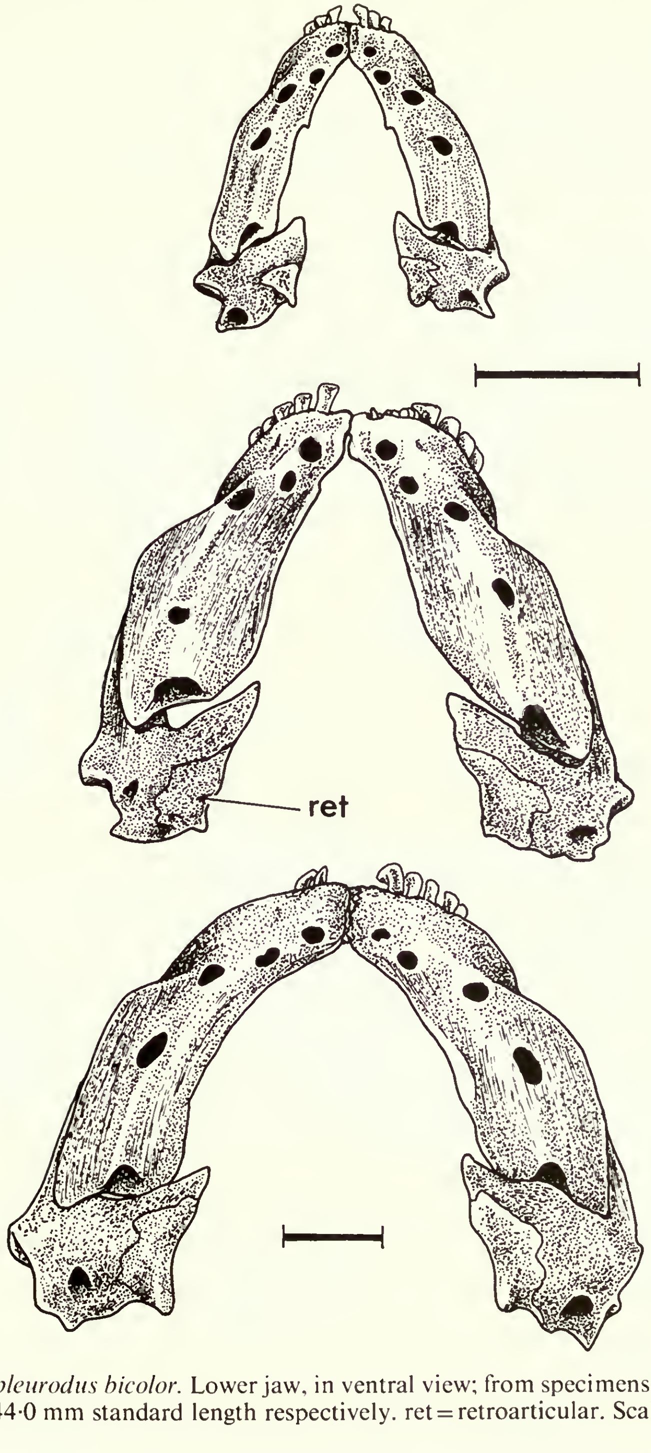

Fig. 9 *Macropleurodus bicolor*. Lower jaw, in ventral view; from specimens 58·0 (top), 115·0 and 144·0 mm standard length respectively. ret = retroarticular. Scale = 3 mm.

A comparison and assessment of other anatomical features in *Macropleurodus bicolor* and *Chilotilapia rhoadesi*

The superficial characters, body form and meristic characters of the two taxa (see Boulenger, 1915; Regan, 1922*a*), apart from the densely and almost completely scaled caudal fin in *C. rhoadesi*, and differences in coloration, do not provide any features of value for testing a hypothesis of close relationship.

The caudal fin character, which Regan (1922*a* & *b*) and Trewavas (1949) used as evidence for close interrelationship of the Malawi haplochromines and their distinctness from those of Lake Victoria, will be discussed later (p. 228).

In their live coloration (see Greenwood, 1956:308–310 for *M. bicolor*; Axelrod & Burgess, 1977:176–177 for *C. rhoadesi*), and in the colour-patterns of preserved specimens (Greenwood, 1956:308–310; Trewavas, 1935:110) the taxa are quite distinct. Trewavas (1935:110) suggested that the colour pattern of *C. rhoadesi* might indicate its relationship with another Malawian endemic, *Haplochromis euchilus* Trewavas. This feature will be discussed later, together with Regan's ideas on colour-patterns as indicators of a monophyletic origin for the Malawi haplochromines (Regan, 1922*a*:686).

Macropleurodus bicolor exhibits a form of sex-limited polychromatism in which about 30 per cent of females have a piebald coloration (Greenwood, 1956:309). Similar polychromatism occurs in several endemic species of Lake Victoria haplochromines, not all of which appear to be closely related to one another or to *Macropleurodus* (Greenwood, 1974:53–54;

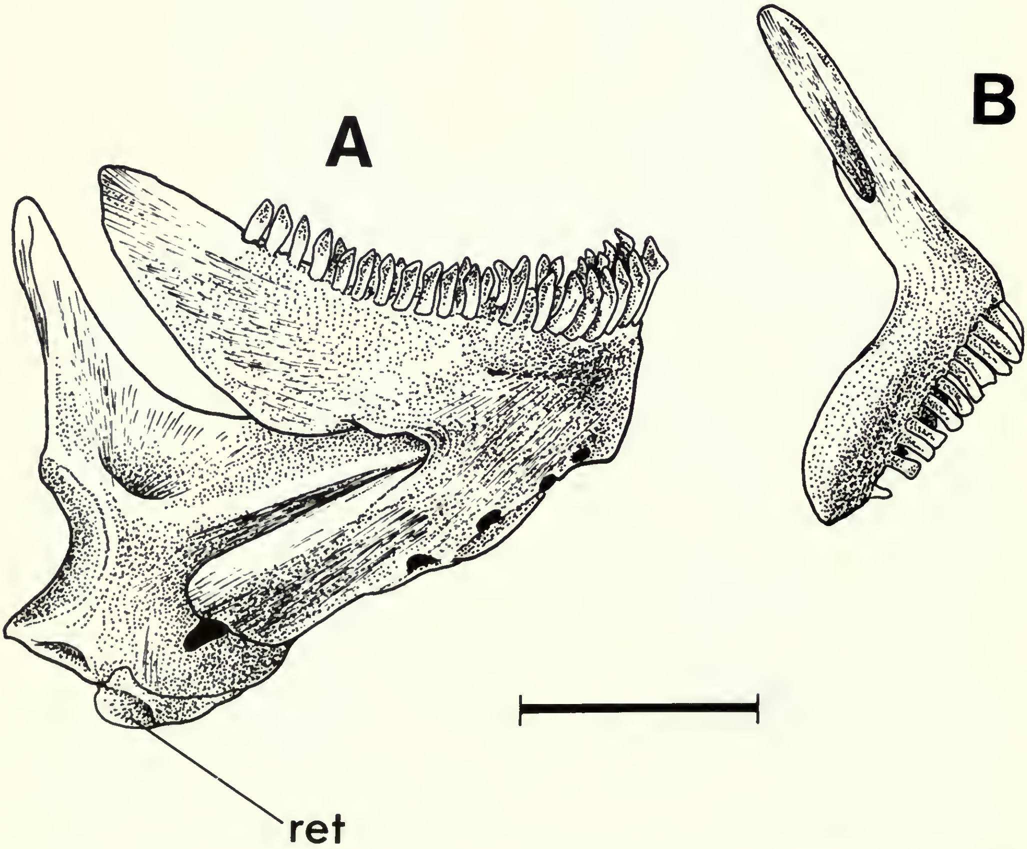

Fig. 10 *Chilotilapia rhoadesi.* A. Dentary and B. Premaxilla; both in right lateral view. ret = retroarticular. Scale = 3 mm.

also 1980, for revised views on the relationships of the various species). Sex-limited polychromatism, involving both similar and different colour patterns, has also been recorded in several Malawi endemics (Fryer & Iles, 1972) but not in *Chilotilapia.*

Adult male *Macropleurodus* have, on the anal fin, a number of scarlet 'egg-dummies' of the true ocellar type (see Greenwood, 1979:274–5). As far as I can tell from colour photographs and from written descriptions, true ocellar markings are lacking in male *Chilotilapia.* Instead, the anal fin carries a few yellowish spots resembling those on the dorsal and caudal fins, a not uncommon condition amongst Malawi haplochromines, but one not recorded in Lake Victoria.

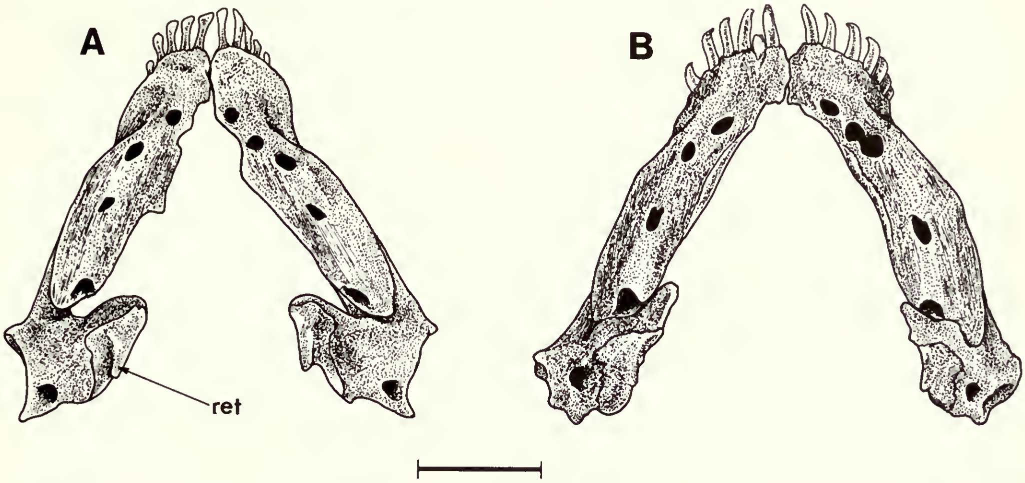

Fig. 11 Lower jaw, in ventral view, of: left, *Paralabidochromis crassilabris* (105 mm standard length); right. '*Haplochromis' euchilus* (91 mm standard length). ret = retroarticular. Scale = 3 mm.

At a deeper anatomical level, intergeneric comparisons were made of the jaw and branchial musculature, and of the cranial and axial skeletons. The latter will be considered first.

There is a close similarity in the morphology of the dentary and premaxilla in *Chilotilapia* and *Macropleurodus,* as there is in the form of the maxilla, a stout and somewhat foreshortened bone in both genera.

The dentary (Fig. 10) too is short, deep and stout, with a noticeably inflated region surrounding its division into ascending, coronoid, and horizontal arms. The principal intergeneric difference lies in the greater posterior extension of the outer tooth row in *Chilotilapia*, the row continuing backwards to a point almost two-thirds of the way up the coronoid process. In *Macropleurodus* the teeth do not extend, or extend for only a short distance, onto the process.

The premaxilla (Fig. 10) is basically similar in both genera, although in *Macropleurodus* the dentigerous arm is somewhat less inflated. Also, in that genus one or both dentigerous arms are distinctly arched in the vertical plane (see Greenwood, 1956:306–7; 1980:83); this apparently is an autapomorphy peculiar to *Macropleurodus.*

Certain derived features in the dentary of *Chilotilapia* and that of *Macropleurodus* are shared with some Malawi taxa, (*'Haplochromis' euchilus* Trewavas [see first para. p. 228] and various *Labidochromis* species), with members of the *Paralabidochromis–Ptyochromis* lineage in Lake Victoria (see below), and with at least one species, *Lobochilotes labiatus* Blgr, from Lake Tanganyika.

These derived features, discussed by Greenwood (1980:93–94), are concerned chiefly with the foreshortened lower jaw, the marked bullation of the dentary in the area surrounding its bifurcation (see above), the pronounced medial curvature of its lateral walls, and the way in which the anterior part of the outer tooth row has a strong ventral dip in its line of insertion on the bone.

In Lake Victoria, these characters are shared by members of a lineage which includes *Macropleurodus* and the genera *Paralabidochromis* and *Ptyochromis*. These taxa, in turn, are part of a larger group, the so-called *Psammochromis–Macropleurodus* superlineage (Greenwood, 1980:93–94).

Resemblances in lower jaw form between *Chilotilapia* and *Macropleurodus* on the one hand, and the various Malawi, Victoria and Tanganyika taxa on the other, are most apparent when specimens of *Chilotilapia* and *Macropleurodus* less than 70 mm SL are used as a basis for comparison, irrespective of specimen size in the other species involved. Within the Lake Victoria lineage, overall resemblance with *Chilotilapia* and *Macropleurodus* is closest when comparisons are made with members of the genus *Paralabidochromis* (Fig. 11), less so when the species of *Ptyochromis* are used (see Greenwood, 1980:60–72; 92–94). A level of similarity equal to that existing with *Paralabidochromis* is found when small *Chilotilapia* and *Macropleurodus* are compared with specimens of various *Labidochromis* species, *'Haplochromis' euchilus* and *Lobochilotes* (Fig. 11).

With growth, the dentary in both *Chilotilapia* and *Macropleurodus* changes its outline shape (see above, p. 218), and thus, superficially, comes to resemble less closely the dentary in these other species. The other derived features remain unaltered, however.

In the ontogeny of their jaws, at least over the size range of available specimens, *Chilotilapia* and *Macropleurodus* could be described as passing first through a *Paralabidochromis–Labidochromis* stage and then an *'H'. euchilus–Lobochilotes* stage. From that point onwards the jaws in *Chilotilapia* and *Macropleurodus* begin to broaden anteriorly, taking on the wide-based U shape characteristic of the adults in both taxa. Simultaneously the autapomorphic features of each genus begin to be manifest (see above p. 223).

Neurocranial shape and architecture is similar in *Chilotilapia* and *Macropleurodus*, but with the former having a taller and more expansive supraoccipital crest. The crest also con-

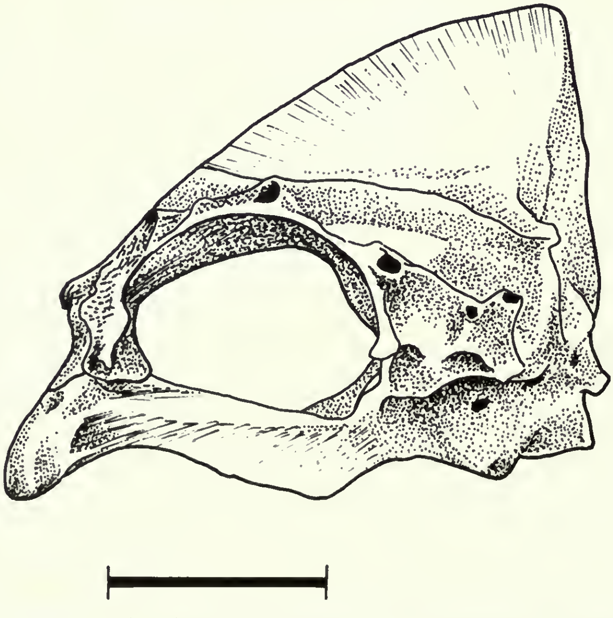

Fig. 12 *Chilotilapia rhoadesi* Neurocranium in left lateral view. Scales = 10 mm.

tinues further forward than it does in *Macropleurodus,* with the result that the slope of its anterior margin is continuous with the slope of the ethmovomerine skull region (Fig. 12); in *Macropleurodus* this line is interrupted (cf. Fig. 12 with fig. 54 in Greenwood, 1980).

The *Macropleurodus–Chilotilapia* skull can be considered derived relative to that in *Astatotilapia* species and in several cranially generalized haplochromine lineages (see Greenwood, 1979; 1980). It approximates closely to the skull form in some *Ptyochromis* species of Lake Victoria, e.g. *P. annectens* (Regan), *P. sauvagei* (Pfeffer), and *P. granti* (Blgr). *Ptyochromis,* it will be recalled, is a member of the *Psammochromis–Macropleurodus* superlineage to which the genus *Paralabidochromis,* mentioned above in connection with lower jaw morphology, also belongs. Like *Ptyochromis,* both *Chilotilapia* and *Macropleurodus* are mollusc-eaters which 'shell' their prey orally (see Fryer & Iles, 1972:75; Greenwood, 1956; 1974:69–72; 1980:60–67). Thus, jaw form and skull shape in all these species could well be correlated characters forming part of a functional unit. The similarities in jaw morphology existing between non-mollusc eating members of the *Psammochromis-Macropleurodus* superlineage (i.e., in this context, the *Paralabidochromis* species), *'Haplochromis' euchilus*, the *Labidochromis* species and *Lobochilotes labiatus* on the one hand, and *Macropleurodus* and *Chilotilapia* on the other, are not susceptible to this explanation.

There has, in the past, been some confusion about the nature of the pharyngeal apophysis in *Chilotilapia* (see Regan, 1922*a*:676; Trewavas, 1935:69–70; Greenwood, 1978:316). The growth series of *Chilotilapia* neurocrania now available help both to clarify that situation and to weaken further the idea of a rigid division between the *'Haplochromis'* and *'Tilapia'* apophyseal types (see discussion in Greenwood, 1978:321).

In a *Chilotilapia* skull of 16 mm neurocranial length, i.e. skull length measured from the anterior tip of the vomer to the posterior face of the basioccipital condylar surface, the apophysis is structurally intermediate between the *'Tilapia'* and the *'Tropheus'* types defined by Greenwood (1978:299–305). Its articulatory facet is formed from the parasphenoid with a small contribution from the basioccipital. The latter, however, has a rounded surface and thus does not seem to form part of the functional articulatory surface. The basal part of the apophysis, i.e. the prootic and basioccipital, is rather inflated; when viewed from behind the entire structure is low and broad.

At a neurocranial length of 23 mm, the apophysis is intermediate between the *'Tropheus'* and *'Haplochromis'* types. The basioccipital makes a small but definite contribution to the articulatory surface (about a third of its area), and the apophyseal base is narrow and less inflated than in the 16 mm skull.

In the largest skull examined, 39 mm neurocranial length, the basioccipital contribution to the articular surface has increased somewhat so that the surface is clearly of the *'Haplochromis'* type (see also Greenwood, 1978:316), as is the narrow, near-vertically walled apophyseal base formed from the prootic and basioccipital.

The apophysis in the smallest available skull of *Macropleurodus,* 20 mm neurocranial length, has an articulatory surface of the *'Haplochromis'* type, although the base of the apophysis is somewhat inflated. In larger skulls, to 25 mm neurocranial length, the base narrows, its walls become more nearly vertical, and there is an increase in the extent to which the basioccipital contributes to the articulatory surface.

The palatopterygoid arch and the suspensorium are similar in *Chilotilapia* and *Macropleurodus,* although both are relatively deeper in *Macropleurodus.* The palatopterygoid arch, when compared with that in *Astatotilapia* and in many other haplochromines, is derived. It is foreshortened, with the lateral face of the metapterygoid deeply concave over most of its area. Like other derived features of the syncranial architecture, this form of palatopterygoid arch occurs in several Lake Victoria species belonging to the *Ptyochromis–Paralabidochromis* assemblage, as well as in *Hoplotilapia retrodens*, another member of the *Psammochromis-Macropleurodus* superlineage; Greenwood, 1980:82. It is also found in certain Lake Malawi taxa, e.g. *Labidochromis* and *Cyathochromis*, and in some species from Lake Tanganyika as well.

Judging from that pattern of distribution, it seems that this type of palatopterygoid arch is one correlated with a foreshortened skull and the development of a powerful *adductor mandibulae* muscle complex.

The total number of vertebrae, excluding the fused $PU_1 + U_1$ elements, has the same range, 29 or 30, mode 30, in both genera. However, in the samples examined, *Chilotilapia* has modal counts of 14 abdominal and 16 caudal centra, compared with 13 and 17 centra respectively in *Macropleurodus.*

Myologically, the jaw and branchial musculature, and the associated ligaments in both *Chilotilapia* and *Macropleurodus* are similar, and are close to the presumed generalized condition found in *Astatotilapia elegans* (see Anker, 1978; Stiassny, 1981; Greenwood, 1983).

The A_1 and A_2 divisions of the *adductor mandibulae* muscle complex in *Chilotilapia* and *Macropleurodus* are relatively stouter than those in *A. elegans,* but are comparable with the condition found in *Ptyochromis* species, which taxa are also oral-shelling mollusc eaters (Greenwood, 1974; 1980).

The A_3 division of the *adductor mandibulae* in *Chilotilapia* is more slender than in *Macropleurodus*, and its outline is bobbin-shaped rather than triangular.

Chilotilapia differs from *Macropleurodus* in having three rather than two divisions to the ethmo-palatine ligament. *Macropleurodus,* like the majority of Lake Victoria haplochromines, has the long posterior division of the ligament running from the palatine bone to the posterior, i.e. orbital, face of the lateral ethmoid, and the shorter division running to the anterior face of that bone. In *Chilotilapia,* a third division lies between the other two, whose attachments are as in *Macropleurodus,* and attaches to the ventral face of the lateral ethmoid.

There is little comparative information on these ligaments in cichlid fishes, and thus the significance of their intergeneric differences cannot be assessed. A tripartite ethmo-palatine ligament does occur in several Malawi taxa I examined, and in some Tanganyika species as well. The condition is rarely encountered in Lake Victoria haplochromines although, and perhaps significantly, it is present in one oral-sheller, *Ptyochromis annectens* (Regan).

Gill-arch musculature in *Chilotilapia* and *Macropleurodus* is of the generalized type (see Liem, 1981; Greenwood, 1983). There are slight differences in the degree to which certain muscles are developed in the two genera. The *levatores externi,* especially the fourth pair, are larger in *Chilotilapia,* and the *transversus dorsalis epibranchialis* 2 is more tendinous in *Macropleurodus.* Both genera have the first *levator externi* muscles well-developed, with musculose rather than tendinous insertions.

Because relatively little information is available on the comparative myology of the Cichlidae, the information derived from *Chilotilapia* and *Macropleurodus* provides no data of positive value in a phylogenetic context. Negatively, however, since their myology compares closely with the generalized condition, it is possible to say that no uniquely apomorphic features are shared by the two genera.

Indeed, the same can also be said for the apomorphic osteological features discussed earlier; all are found in other taxa from Lakes Malawi, Tanganyika and, especially, in species from Lake Victoria. This rather skewed geographical pattern of apomorphy distribution could, however, be artefactual since more is known about the osteology in species from Lake Victoria than in those from the other lakes.

Be that as it may, the only derived features uniquely shared by *Chilotilapia* and *Macropleurodus* are those relating to tooth morphology and dental patterns in adult and near-adult fishes (see pp. 211–218).

Since these dental apomorphies apparently are not congruent with any other derived characters uniquely shared by the two taxa, they cannot be considered homologous, i.e., true synapomorphies, and must therefore be treated as homoplasies (see discussion in Patterson, 1982).

It remains to be determined whether these homoplasies resulted from parallel or from convergent evolution, and also to assess what phylogenetic significance can be given to those apomorphic features shared by *Chilotilapia, Macropleurodus* and the other taxa mentioned above.

Discussion and conclusions

Before considering these various issues, it is necessary to review current ideas on the origin and relationships of cichlids from Lakes Malawi, Victoria and Tanganyika.

Prior to Regan's (1920; 1922*a* & *b*) revisionary studies on these fishes, and his fundamental reorganization of their generic classification (Regan, 1920), no meaningful speculations or hypotheses could be generated about the origin and relationships of the lake flocks.

Regan based his supraspecific grouping of African cichlids on the nature of the neurocranial apophysis on which the upper pharyngeal bones articulate, a scheme he first worked out on the taxa from Lake Tanganyika (Regan, 1920). On the basis of this character, the majority of Malawian and Victorian species were placed in Regan's *'Haplochromis'* divison. The Lake Tanganyika species, on the other hand, were more equally shared between this division and the so-called *'Tilapia'* one. Since Regan considered these two divisions represented a fundamental dichotomy in the phylogeny of the Cichlidae, his views on the relationship of taxa, endemic and otherwise, from the three lakes were influenced accordingly. In particular this meant that resemblances between any member of the *'Tilapia'* group and another of the *'Haplochromis'* group could only be interpreted as the result of convergent evolution.

Trewavas (1935) followed Regan's scheme of supraspecific grouping when she revised the Malawi cichlids, although she transferred four taxa, one of which was *Chilotilapia,* from the *'Tilapia'* to the *'Haplochromis'* division.

Recent research (Wickler, 1963; Fryer & Iles, 1972; Liem & Stewart, 1976; Greenwood, 1978, 1983) strongly indicates that a basic phylogenetic division of African cichlids on apophyseal structure cannot be substantiated (see also observations on the apophysis in *Chilotilapia,* p. 225 above).

Abandoning the pharyngeal apophysis as a critical character for determining major cichlid groupings has, in fact, little effect on the problem of *Chilotilapia–Macropleurodus* interrelationships since definitive apophyseal structure in both genera is of the *'Haplochromis'* type. It does, however, affect problems concerned with the relationship of other closely similar taxon pairs, or trios, shared between Lakes Malawi, Victoria and Tanganyika. As examples of taxa whose phyletic status requires reexamination on the basis of other features, one can cite the supposedly convergent *Petrotilapia* (M) and *Petrochromis* (T), *Tropheus* (T) and *Labeotropheus* (M), and *Lobochilotes* (T), *'Haplochromis' euchilus* (M) and *Paralabidochromis chilotes* (V).

Regan (1922*b*:158), working within the framework of his strictly dichotomous divisions of the cichlids, believed . . . 'The indications are that the endemic Nyassa (=Malawi) cichlids have originated in the lake from about half-a-dozen ancestral forms'.

Later, Trewavas (1949) supported Regan's concept of an oligophyletic origin for these fishes. After quoting Regan's statement reproduced above, she carried the argument further by concluding, with regard to the endemic Malawian genera, that the '. . . balance of evidence (is) in favour of Nyassa relationship for all of them'. Indeed, Trewavas (*op. cit.*) specifically rejects Myer's (1936) suggested relationship of the Malawian genus *Pseudotropheus* with the Tanganyika *Simotes,* because the two taxa have different types of pharyngeal apophyses.

Regan (1922*a* & *b*) did not discuss the possible interrelationships of his suggested 'half-a-dozen' ancestral species. He did, however, consider that the numerous endemic *'Haplochromis'* species of Lake Malawi '. . . appear to form a natural group and have evidently evolved in the lake from one or a few ancestral forms' (Regan, 1922*b*:158). This idea was based largely on one feature which, as far as Regan could ascertain, was shared by most Malawi *'Haplochromis'* species, namely a caudal fin densely covered in small scales. Regan contrasts this condition with that in the *'Haplochromis'* species of Lake Victoria where the '. . . caudal fin is scaly only on its basal half'.

The genus *Haplochromis* has now been restricted to five species, none of which occurs in Lake Malawi (Greenwood, 1980). No attempt has yet been made to subdivide the Malawian species formerly classified in *Haplochromis*; these are referred to here under the epithet *'Haplochromis'*.

In support of his ideas about the Malawi *'Haplochromis'* species being a natural group, Regan (*op. cit.*) drew attention to the fact that the caudal fin in these species is more or less distinctly emarginate (rounded or truncate in Victoria species) and that a few distinctive types of coloration, none of which occurs in Lake Victoria, are prevalent amongst the Malawi fishes. Here again, Trewavas (1935; 1949) accepted Regan's arguments, and expanded the scope of the supposed natural group defined by these characters to include the endemic haplochromine genera of Lake Malawi. Thus, at least by implication, all the haplochromine taxa of Malawi were assumed to be members of a natural group. From this it would follow, again by implication, that the ancestral forms were more closely related to one another than to any other taxa. Also, but neither Regan nor Trewavas is explicit on this point, the argument would assume the caudal fin characters to have evolved within the Lake because no extant fluviatile species show these features. Trewavas (1949) does, however, note, but makes no further comment on, the absence of a fully scaled caudal fin in *'Haplochromis' callipterus* (Günther), a species which she thought to be a likely representative of the '... ancestor of many (*'Haplochromis'*) species of Nyasa'.

The validity of the caudal fin characters as evidence for a natural group in Lake Malawi is weakened by a fact which neither author mentions, that is, the occurrence of a densely and completely, or almost completely, scaled caudal fin in several endemic Tanganyika genera, some of which also have the fin forked or emarginate, e.g. *Petrochromis, Simochromis, Tropheus, Lobochilotes, Eretmodus, Lamprologus,* and *Cyphotilapia*; personal observations based on a by no means comprehensive sample of the Lake Tanganyika species. Interestingly, four of these Tanganyika genera have been associated in a 'convergent' relationship with taxa from Lake Malawi (see above, p. 227).

Finally, and perhaps most significantly, it must be noted that the four endemic species of *Oreochromis* (= *Tilapia* of Trewavas, 1935 & 1949) in Lake Malawi also have densely and completely scaled caudal fins. None of these species is in any way closely related to the Malawi haplochromines.

Such a character distribution pattern, and especially its inclusion of the endemic Malawi *Oreochromis* species, would seem to invalidate the character's use as a means of identifying the Lake Malawi haplochromines as a 'natural group'.

The shape of the caudal fin margin is also of doubtful validity in this context. To start with, it shows a quite considerable range of variation within the Malawi taxa, in some of which the nature of the fin margin scarcely differs from the condition found in certain Lake Victoria species. In that Lake, *pace* Regan, a rounded caudal margin is rare, the modal condition ranging from subtruncate to truncate; a few species even have a slight but distinctly emarginate fin (compare figures in Greenwood, 1982*a* with those in Regan, 1922*a*). Truncate and emarginate fins, as well as subtruncate and rounded ones, occur amongst the Lake Tanganyika endemics, sometimes with more than one type present in a single genus.

Again, one is apparently faced with a character of doubtful phylogenetic validity. Not only is this so for the reasons given above but, like the scaly caudal fin, because it is not congruent with other and well-substantiated synapomorphies shared by the various taxa involved.

The absence of a fully scaled caudal fin amongst the Lake Victoria cichlids, contrasted with the near universal occurrence of that trait in Malawi cichlids, and its presence among some but not all Tanganyika taxa, nevertheless requires explanation. The answer, however, like that explaining the occurrence of predominant but different kinds of caudal fin margins in each of the different lakes, is unlikely to be provided by the data currently available.

Regan's (1922*a*:686) view that the prevalence of a few distinctive types of coloration among the Malawi haplochromines corroborated the other indications of their evolution '... within the lake from a single ancestral form ...', can also be challenged. Granted, there are distinctive colour patterns, i.e. striping, barring etc., and some distinctive types of overall coloration not found in the fishes of Victoria or Tanganyika. But, since these features are not shared by every member of the Malawi flock, they cannot be taken to indicate monophyly for all the species of the Lake. Their value as indicators of relationship lies at a much lower level of universality.

The absence of true anal ocelli in male *Chilotilapia,* and in most Malawi haplochromines, contrasted with their presence in males of, apparently, all Victoria haplochromines, poses an insoluble question with regard to phylogenetic histories (see Greenwood, 1979:274–276). It is a character that has not yet received sufficient study to permit its evaluation in that context. Whether true ocelli be a derived or a plesiomorphic feature, the fact that both ocellar and non-ocellar anal markings are present in Malawi haplochromines would argue against a monophyletic origin for the flock as a whole.

In short, I would suggest that none of the characters so far proposed in support of a mono- or even oligophyletic origin for the Malawi haplochromines is valid for that purpose. Since, despite an extensive search, I can find no valid characters to replace them, the case for a monophyletic origin of the Malawi haplochromines must, for the moment, remain unsubstantiated.

Research on the haplochromines of Lake Victoria has also failed to reveal a single synapomorphy indicative of a monophyletic origin for those taxa either (Greenwood, 1979; 1980). What is suggested, however, is the presence of several distinct monophyletic lineages whose distributions include not only Lake Victoria but Lakes George, Edward and Kivu as well. Each of these lineages is distinguished by, at best, two or three synapomorphies. In other words, there is a low level of interlineage differentiation, with the residual, i.e. plesiomorphic, characters being common to most haplochromine taxa whatever their geographical distribution may be.

Perhaps significantly, it is with one of the Victoria lineages, the *Paralabidochromis-Ptyochromis-Macropleurodus* complex within the *Psammochromis-Macropleurodus* superlineage, that *Chilotilapia* shares the greatest number of apomorphic characters (see Greenwood, 1980:91–94; & p. 223 above). Furthermore, there are at least two taxa in Lake Malawi, *Labidochromis* and *'Haplochromis' euchilus,* and one from Lake Tanganyika, *Lobochilotes labiatus* Blgr, which also share a number of these features. In none of these latter taxa can I identify any synapomorphies shared with Lake Victoria lineages other than the *Paralabidochromis-Macropleurodus* one, nor any which might suggest a relationship, above the sister-species level, with taxa from, respectively, Lake Malawi or Lake Tanganyika.

Parenthetically it should be noted that some of the oral features shared by these taxa also occur in two other Lake Victoria lineages, namely *Neochromis* and *Lipochromis* (see discussion in Greenwood, 1980: 52 & 91–94; also p. 223 above). It has been argued (Greenwood, *op. cit.*) on the basis of derived dental features shared by members of the *Psammochromis-Macropleurodus* superlineage, and others uniquely characterizing *Neochromis* and *Lipochromis,* that the similarities in jaw morphology shared by these two taxa with members of the former group were independently evolved. Since the derived dental features of the *Psammochromis-Macropleurodus* group taxa are manifest in *Labidochromis, 'H'. euchilus, Lobochilotes* and *Chilotilapia,* the same argument, that is convergence, can be applied to account for their similarities in jaw morphology with *Neochromis* and *Lipochromis.*

Work in progress supports the suggestion of several derived characters being shared by the supposedly 'convergent' Malawi–Tanganyika taxon pairs mentioned on p. 227, and thus that they too may be more closely related than was previously thought. Here, however, it has so far proved impossible to identify any association with a particular lineage from Lake Victoria.

In view of these character distribution patterns, and because the hypothesized monophyletic origin for each lake flock cannot be substantiated, consideration should be given to an alternative hypothesis. Namely, that the flocks are of polyphyletic origin and that many of the lineages within a flock occur in more than one lake. The pattern of apomorph character distribution in, for example, *Macropleurodus* (V), *Chilotilapia* (M), *'Haplochromis' euchilus* (M) and *Lobochilotes* (T) would be explicable on that basis.

Since Lakes Victoria, Malawi and Tanganyika are of different ages (Greenwood, 1982*b*) and are geographically distant from one another, it is probable that the progenitors of the lineage representatives in each lake would have been different but closely related species. This evolutionary pattern would mean that, despite the ultimate monophyly of a lineage, at the lowest hierarchical levels sister taxa would occur sympatrically. For example, the Lake Victoria members in the lineage cited above would be more closely related to one another than to species in the other lakes, and similarly for the taxa from Malawi and Tanganyika.

On the basis of that argument, the homoplastic dental resemblances between *Chilotilapia* and *Macropleurodus* (see p. 218) are parallelisms, and the nearest relatives of the two taxa should be found in Lakes Malawi and Victoria respectively.

As has already been suggested, the relationships of *Macropleurodus* are apparently with *Paralabidochromis* and *Ptyochromis,* although, for the moment no finer resolution is possible (see Greenwood, 1980:92).

The closest relatives of *Chilotilapia* would, in my view, seem to be *Labidochromis* and, as Trewavas (1935:110) suggested, *'Haplochromis' euchilus.* Again, any finer resolution must await further research, as must the resolution of relationships for *Lobochilotes labiatus,* at present seemingly the sole representative of the lineage in Lake Tanganyika.

If this scheme of relationships is accepted, then the generic status accorded to *Chilotilapia* and *Macropleurodus* by earlier workers is justified, despite the close similarity of the two taxa (see p. 210). I would also agree with their suggestion that the resemblances are homoplastic ones, but not, as was also suggested, the results of convergent evolution.

What I would argue against is the reasoning used by those workers for separating the taxa at more than the species level, namely the level and nature of phyletic differences between the two cichlid faunas to which the taxa belong. There would seem to be no grounds for assuming that each lake flock is of monophyletic origin, or that each flock is, phylogenetically speaking, a natural group. On the contrary, there seem to be grounds for thinking that each flock is composed of several lineages, and that most of these lineages have a geographical distribution which cuts across the present day lake boundaries. This, of course is not to deny that some lineages may have evolved in, and are endemic to, a particular lake, or that some lineages may be common to only Lakes Malawi and Tanganyika (see p. 227).

Regan's (1922*b*:158) postulated half-a-dozen ancestors for the Malawi haplochromine flock could, in essence but perhaps not magnitude, be nearer the mark than his and other workers' ideas on the flock's monophyly (Regan, 1922*a* & *b*; Trewavas, 1935 & 1949; Greenwood, 1974), and may well represent the situation in other lakes as well (Greenwood, 1980). Only a great deal more, and critical, work on the cichlids of all three major lakes will serve to test those suggestions.

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NATURAL HISTORY

Deuterammina (Lepidodeuterammina) subgen. nov., and a redescription of *Rotalina ochracea* Williamson (Protozoa: Foraminiferida)

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I. A lectotype for *Rotalina ochracea* Williamson

Rotalina ochracea Williamson (1858) was based on three specimens obtained from 'sand from Shetland'. Spiral and umbilical views, probably of the same specimen, were illustrated (figs 112, 113) and the species was described in the classic monograph *On the Recent Foraminifera of Great Britain* as follows (p. 55)...

> Shell trochoid, depressed; slightly convex and smooth superiorly, correspondingly concave inferiorly; with about two and a half convolutions; arcuate; filled with brown animal matter, which is pale and translucent in the ultimate segments, but very dark and opaque in those near the umbilicus. Septa smooth in one specimen, a little elevated in another; broad, and of light ochraceous yellow, contrasting richly in the dark tint of the segments. The connecting spiral has the same ochraceous line. Inferiorly the segments of the last convolution extend nearly to the umbilicus, concealing the rest. Segments depressed or concave. Septal lines arcuate, flexuose and very prominent.

Balkwill & Millett (1884) recognised the agglutinated nature of the test and transferred it to *Trochammina.* For a history of *Trochammina,* see Hedley *et al.,* 1964 : 418. Although *Trochammina ochracea* (Williamson) is one of the most frequently reported species of the genus (see for instance, Heron-Allen & Earland, 1915; Cushman, 1920; Rhumbler, 1938; Höglund, 1947; Todd & Low, 1961; Murray, 1971; Haynes, 1973; Lutze, 1974) its detailed morphology is for the most part poorly known. Williamson's figured specimen is, unfortunately, not in the remaining part of his collection in the British Museum (Natural History) and must be considered lost. The other two specimens (syntypes) are, however, extant and were figured by Hedley *et al.* (1964; figs 2, 3). In spite of this work, the species continues to be largely misidentified and it is now thought necessary to designate a lectotype and describe and illustrate the species afresh, using the benefits of scanning electron microscopy (SEM). Particular attention is paid to details of the apertures, in the light of recent advances in trochamminid taxonomy (see p. 236, below). The lectotype chosen bears the BMNH reg. no. 1963.2.19.16 and is illustrated in Figs 1–8, 10, herein.

DESCRIPTION. (Lectotype). Test a concavo-convex, strongly compressed ('watch-glass' shaped) dextral trochospire comprising some 26 chambers arranged in almost 3 whorls, with 8 chambers in the final whorl. In outline the test is oval and slightly lobate; the periphery is rounded-compressed. Proloculus ellipsoidal 15 × 10 μm in diameter. The chambers increase rapidly in size, those of the last whorl almost doubling in tangential diameter. Sutures curved and weakly depressed in the last whorl. Sutures on umbilical side strongly

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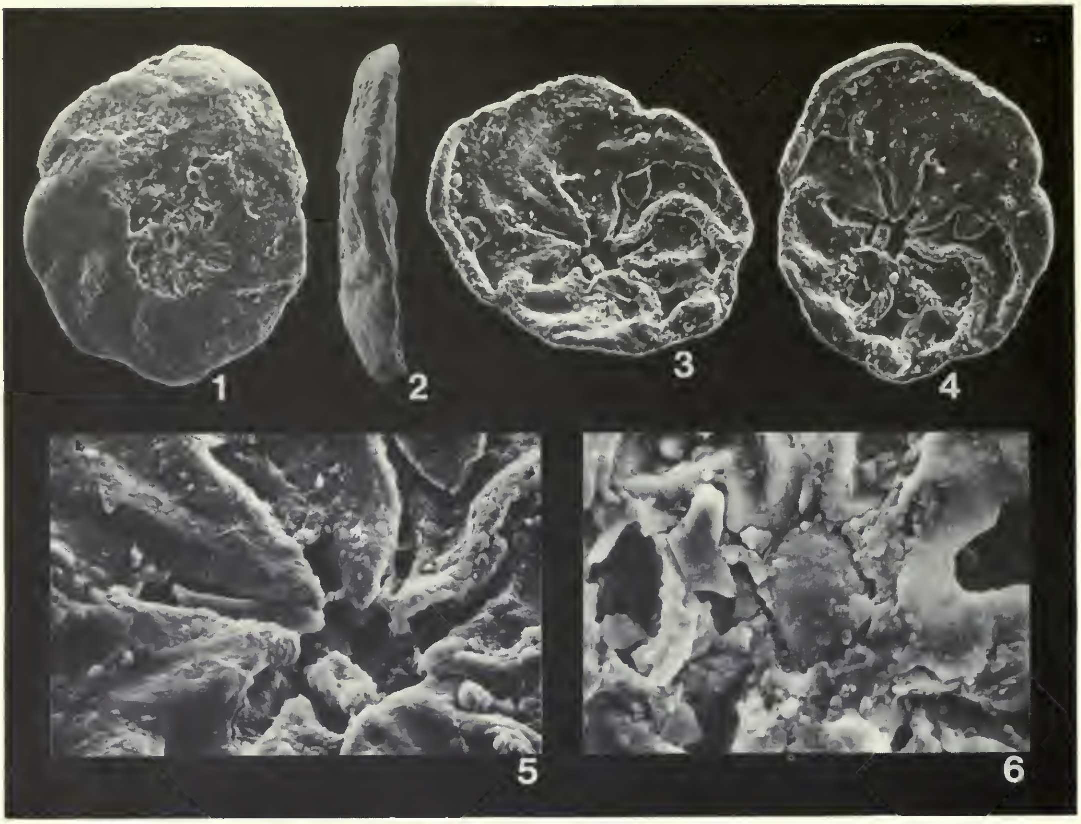


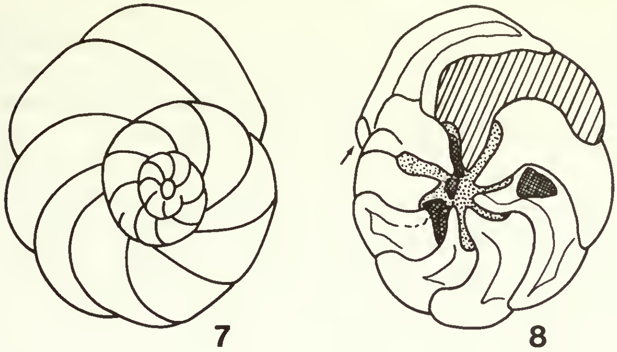
Figs 1–6 *Deuterammina (Lepidodeuterammina) ochracea* (Williamson) subgen. nov. Lectotype (1963.2.19.16). Figs 1–4, spiral, edge, oblique-umbilical and umbilical views; 5, details of umbilical depression seen obliquely; 6, early enrolment (note ellipsoidal proloculus). Figs 1–4, ×175; fig. 5, ×500; fig. 6, ×1250.

Chosen from Williamson's remaining two syntypes, labelled 'Sand from Shetland', off N. Scotland, in shallow water. Previously figured (drawing) by Hedley *et al.*, 1964, fig. 3 : 2.

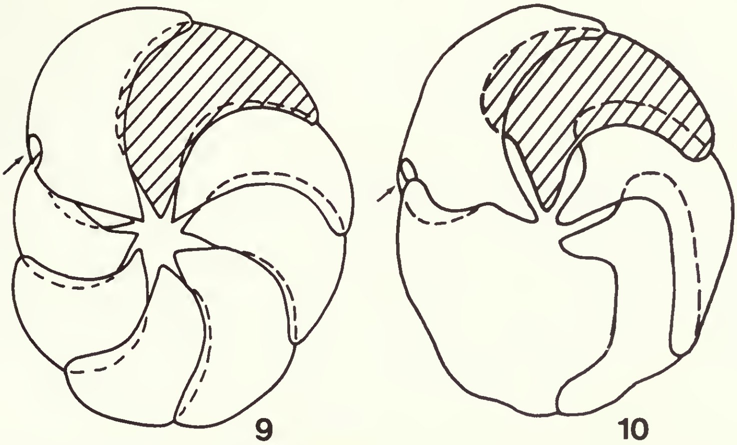
curved. Umbilicus narrow, open, star-shaped; chambers overlapping with inflated proximal margins and pointed umbilical extensions. Two sets of apertures per chamber: a rounded primary extraumbilical aperture situated peripherally and visible only in the last chamber; and a secondary elongate aperture in an umbilical-sutural, posteriorly directed position, below the upturned edge of the pointed umbilical lobe. Wall thin, agglutinated, single-layered and imperforate. Spiral side composed of a rather smooth mosaic of minute, well-cemented, rock flakes and mineral grains. Umbilical side more coarsely granular.

Dimensions. (Lectotype). Maximum and minimum diameter 240×200 μm; thickness (axial height) 45 μm.

Remarks. Spirally, the sutures are not well defined and the thick spiral suture shown by Williamson (1858: fig. 112) has not been observed. On the umbilical side the 8 crescentic chambers each overlap strongly posteriorly, while anteriorly, and distal to the umbilical lobe, the chamber outline undergoes a humpback-like enlargement quite different from other 'watch-glass' shaped forms (compare figs 9 and 10). This widening seems to be an essential feature of the taxon. The umbilical lobes are upturned (fig. 5) and may be compared to the blades of a turbine; underneath them the posteriorly directed secondary apertures open into the umbilical (axial) cavity. The narrow gap between the lobes of the last two chambers is



Figs 7, 8 *Deuterammina (Lepidodeuterammina) ochracea* (Williamson) subgen. nov. Lectotype (1963.2.19.16). Fig. 7, spiral side showing the rapid increase in chamber size during growth, ×175. Fig. 8, umbilical side showing the shape of the penultimate chamber (wide hatching), and the star-shaped umbilical depression (stippled); adventitious matter (crossed hatched). Primary aperture arrowed. ×175. Drawings based on SEM photographs, figs 1, 4.



Figs 9, 10 Diagrams showing form of chamber and umbilical lobe in species of *Deuterammina (Lepidodeuterammina)*. Fig. 9, *D. (Lepidodeuterammina)* sp., illustrated as *Trochammina squamata astrifica* Rhumbler, in Lévy *et al.*, 1974, pl. 1, fig. 9. Fig. 10, *D. (Lepidodeuterammina) ochracea* (Williamson). Lectotype (1963.2.19.16). Shape of penultimate chamber marked by wide hatching and primary aperture by arrows, in both cases. Based on SEM photographs. Fig. 9, ×215; fig. 10, ×250.

about 45 µm long and 7 µm wide. The rim of the primary aperture is slightly damaged and is difficult to see in figs 2–4, its position is indicated in the drawings, figs 8, 10. The chambers of the umbilical side have a tendency to collapse which suggests that the agglutinant is less well cemented than on the spiral side.

II. The systematic position of *Rotalina ochracea* Williamson

Williamson's original coloured illustrations (1858, figs 112, 113) are somewhat stylised, in particular the spiral side (fig. 112) which shows an unusually strong spiral suture. Whatever their shortcomings they served as a standard reference for the identification of many morphologically related, but discrete, small 'watch-glass' shaped trochamminids referred to *Trochammina ochracea,* or to the group of forms typified by *T. ochracea.* Of the many references to this species, only those of Murray (1970, pl. 1, figs 2, 3; 1971 : 37, pl. 11, figs 1–5), Haynes

(1973 : 40, pl. 5, figs 15–18) and Lévy *et al.* (1974, pl. 1, figs 1, 3) are conspecific with the lectotype. Rhumbler (1938) and Höglund (1947) attempted to differentiate taxonomically between these small 'watch-glass' shaped trochamminids, but it is only the advent of SEM that has made it possible to see and illustrate the often minute umbilical and apertural features significant for the classification of this difficult group.

As a result of comparative SEM work on material from the Collections of the R.R.S. *Discovery,* Brönnimann (1976) erected the new genus *Deuterammina,* type species: *Trochammina glabra* Heron-Allen & Earland, to accommodate all previously described species of *Trochammina* which were found to possess two apertures per chamber: a primary, intermarginal and a secondary umbilical opening, the latter situated at the umbilical tip of the chamber in an umbilical-sutural, posteriorly directed, position. By this definition, the overall shape of the test was not taken into consideration at all, and therefore not only forms with rounded peripheries, subglobular chambers and little compression of the test, but also those with almost angular peripheries, strongly compressed chambers and a flattened test, were placed in *Deuterammina.* However, in the course of subsequent work on shallow water deuteramminids (Brönnimann & Whittaker, in preparation) we are now of the opinion that the overall form of the test has also to be taken into account, but only as a classificatory factor of second order to the apertural characteristics. The overall shape of the deuteramminid shell seems to be in direct relationship to the environment in which it lives. In our South Atlantic and Antarctic material flattened 'watch-glass' shaped tests occur in shallow water and tests with subglobular chambers, in relatively deeper water and in the deep sea. The former live attached to a substrate represented by sand grains, seaweed, fragments of bivalves, etc., a moveable biotope in the sense of Rhumbler, 1938. The latter probably live free on or in the uppermost layers of the sediment. These observations are substantiated by findings elsewhere (Brönnimann, 1978; Brönnimann & Maisonneuve, 1980; Lutze, 1974) and by records of *Trochammina ochracea* in the collections of the BMNH from British waters. We therefore propose to formally erect subgenera of *Deuterammina* based on the degree of compression of the text, this subdivision reflecting the environment in which the animals lived. *Deuterammina* (*Deuterammina*) is proposed for all forms typified by *D. glabra* (Heron-Allen & Earland) and *Deuterammina* (*Lepidodeuterammina*) for all the forms with flattened tests typified by *T. ochracea* (Williamson).

Genus ***DEUTERAMMINA*** Brönnimann, 1976,

emended Brönnimann & Whittaker, herein.

Emended generic definition. Test trochospiral, free or attached. Wall agglutinated, single layered, imperforate. Chambers subglobular or axially strongly compressed; without inner structures. Two sets of apertures: primary opening interiomarginal, umbilical-extraumbilical; secondary or supplementary opening at tip of chamber, umbilical-sutural, posteriorly directed.

Type species. *Trochammina glabra* Heron-Allen & Earland, 1932. Recent. Antarctic waters, outer shelf species.

Subgenus ***DEUTERAMMINA (DEUTERAMMINA)*** Brönnimann, 1976

Subgeneric definition. Test trochospiral, free, Chambers subglobular. Primary aperture interiomarginal, umbilical-extraumbilical or extraumbilical; secondary or supplementary aperture at umbilical tip of chamber, umbilical-sutural, posteriorly directed.

Type species. As genus.

Subgenus ***DEUTERAMMINA (LEPIDODEUTERAMMINA)*** subgen. nov.

Subgeneric definition. Test trochospiral, 'watch-glass' shaped, attached. Chambers axially strongly compressed. Primary aperture interiomarginal, extraumbilical; secondary or supplementary aperture at umbilical tip of chamber, umbilical-sutural, posteriorly directed.

TYPE SPECIES. *Rotalina ochracea* Williamson, 1858. Recent. North Atlantic seaboard. Shallow-water species.

NAME. From the Greek, lepido + deuter + ammina, meaning scale-like (shell) with two (apertures) and made of 'sand'. The prefix of the new subgenus in particular refers to the very thin, flattened, concavo-convex nature of the test which we have termed 'watch-glass' shaped.

REMARKS. The primary interiomarginal aperture of *Deuterammina (Deuterammina) glabra* is an elongate narrow umbilical-extraumbilical slit, whereas that of *D. (Lepidodeuterammina)* (e.g. the type species and *D. (L.) labiosa* (Höglund) (1947, pl. 15, fig 6a–c) is either subperipheral in position or (e.g. a new species of *D. (L.)* from Brazil, Brönnimann, in press) of *Trochammina*-type, also a small rounded opening, but this time about halfway between the umbilical cavity and the periphery of the test. Slit-like primary interiomarginal umbilical-extraumbilical or extraumbilical openings have so far not been observed in the 'watch-glass' shaped, attached deuteramminids which seem to be characterised by small, rounded extraumbilical interiomarginal primary openings. These differences in the *form* and *position* of the primary openings are possibly taxonomically of more weight than here accorded but only future work will show whether or not they are of generic, rather than subgeneric significance.

In order to avoid confusion with other attached trochamminids, viz. *Asterotrochammina, Remaneica* and *Rotaliammina, Deuterammina (Lepidodeuterammina)* differs in the following respects: *Asterotrochammina* and *Remaneica* have invaginations (or secondary septa); on the umbilical radial sutures in the former, in the latter, on the spiral side as well. *Rotaliammina* and *D. (Lepidodeuterammina)* do not have invaginations but differ from each other in apertural characters: the latter has a double deuteramminid aperture, a primary, extraumbilical interiomarginal aperture, and a secondary opening at the umbilical tip of the chamber. *Rotaliammina* possesses only a single, umbilically (axially) directed aperture. For further discussion of these genera see Seiglie & Bermúdez, 1977, and Brönnimann, 1978.

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The freeliving marine nematode genus *Sabatieria* (Nematoda: Comesomatidae). I. Two new species from Stonington Island, Antarctica

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Introduction

As a prelude to an eventual review of the genus *Sabatieria,* species from various geographical locations and differing habitats are being examined in detail. This first paper describes two new species from the constantly near-freezing Antarctic waters. The specimens were obtained by SCUBA divers on 30 March 1974 from a small inlet, Back Bay, in the vicinity of the former British Antarctic Survey base at Stonington Island; part of a series of collections detailed elsewhere (Platt, 1979). The substrate was fine sand and stones underlayed at about 2 cm with gravel which prevented coring beneath this depth. The methodology employed for studying the organisms and the abbreviations used in their description have been fully described elsewhere (Platt, 1982).

Systematic descriptions

Sabatieria kelletti sp. nov.
(Figs 1–3)

Material studied. Holotype: ♂1 BM(NH) 1982.5.26. Allotype: ♀1 BM(NH) 1982.5.32. Paratypes: five males BM(NH) 1982.5.27–31; five juveniles BM(NH) 1982.5.33–37.

Locality. 15 m depth, Back Bay, Stonington Island, Antarctica. Lat. 68°12·4′ S, long. 66°59·5′ W.

Measurements (Table 1)

Holotype ♂: $\frac{—\quad 350\quad M\quad 2845}{19\quad 74\quad 87\quad 61}$ 3095 µm; a = 36; b = 8·8; c = 12·4; S = 63 µm

Allotype ♀: $\frac{—\quad 330\quad 1550\quad 3035}{21\quad 74\quad 95\quad 52}$ 3295 µm; a = 35; b = 10·0; c = 12·7; V = 47%

Description. The body narrows suddenly in the region just posterior to the amphid: h.d. 26–33% of the posterior oesophagus c.d. Cuticle punctated: in the lateral field the dots are larger and more irregularly arranged than medially, especially in the oseophagus and tail regions (Fig. 3c, e). The medial dots are more or less arranged in transverse rows (Fig. 3d). In the cylindrical portion of the tail the dots are present but are only very tiny. Somatic setae in four longitudinal files, one on each side of the lateral field: 5–7 µm long and spaced 50–130 µm apart but closer together at the ends than in the middle of the body. In adults there is a subventral row of three more closely spaced cervical setae (Figs 1c, d & 3a). In stage-4 juveniles (J1–4) there are ony two setae in this position (Fig. 1i) and no such setae were observed in what is probably a stage-2 juvenile (J5). There are additional 7–10 µm dorsal and ventral caudal setae in the males (Figs 1f, j & 2f). The tail tip has three terminal setae, one dorsal and two subventral. R1 sensilla papilliform. R2 sensilla short but clearly setiform. R3 sensilla in adults 42–47% h.d.: the same relative length in juveniles. Amphids

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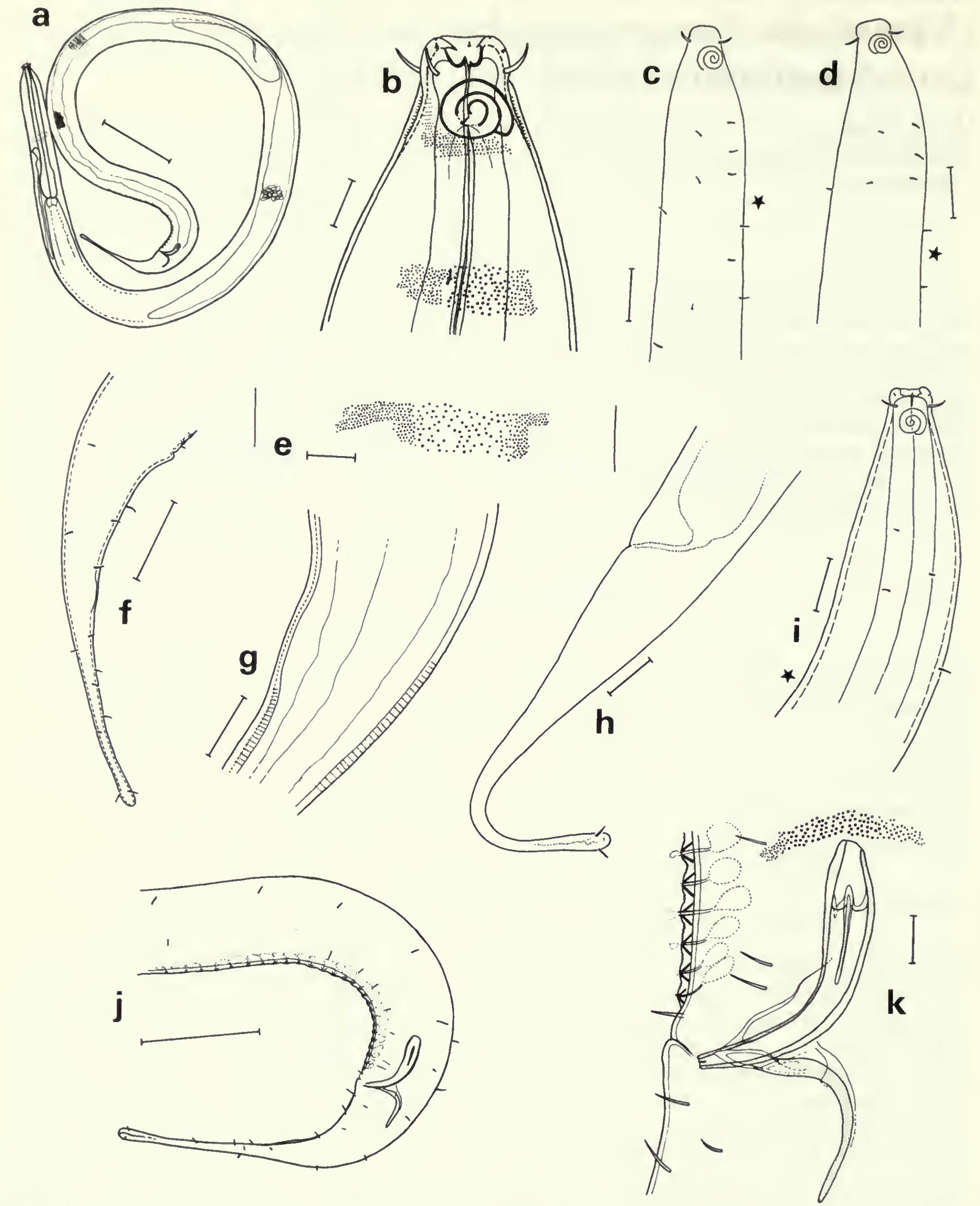


Fig. 1 *Sabatieria kelletti*: (a) ♂1 whole body; (b) ♂1 head; (c) ♂2 anterior region; (d) ♂4 anterior region; (e) ♂1 lateral cuticle pattern mid-body; (f) ♂4 tail region; (g) ♂6 ventral caudal papilla; (h) ♀1 tail; (i) J1 anterior oesophagus region; (j) ♂1 posterior region; (k) ♂1 copulatory apparatus. Bar scales: a = 200 μm; j = 100 μm; f = 50 μm; c, d, h = 30 μm; i = 20 μm; b, e, g, k = 10 μm. Stars in c, d and i indicate ventral side.

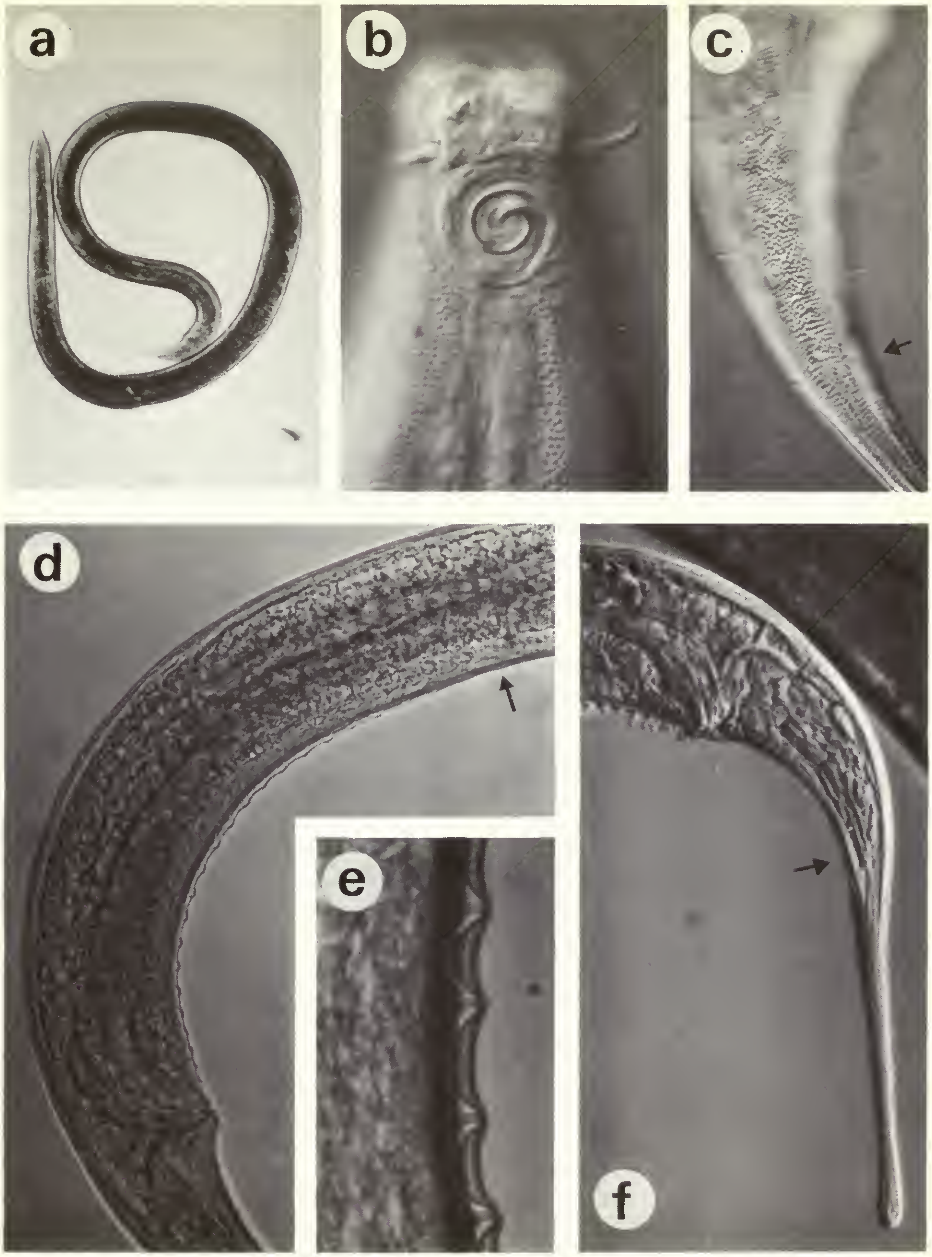


Fig. 2 *Sabatieria kelletti:* (a) ♂1 whole body; (b) amphid and R3 sensilla; (c) caudal cuticle punctations and position of ventral papilla arrowed; (d) posterior region showing precloacal supplements, the anteriormost (24th) is arrowed; (e) detail of supplements; (f) ♂ tail, postcloacal papilla arrowed.

describe $2\frac{1}{2}$ to almost 3 turns; 60–70% c.d. in males; 40% c.d. in female; 45–60% in juveniles. Anterior part of buccal cavity cup-shaped, posterior part not expanded. Oesophagus widens in posterior 20% but is not set-off (Fig. 3b). Nerve ring at 52–54% of oesophagus length. Excretory pore at 61–67% of oesophagus length with a conspicuous ampulla (Fig. 3b). Tail conico-cylindrical; cylindrical part 50–60% of total with a distinct but not greatly swollen tip; 3·6–4·3 a.b.d. in males, 5·0 a.b.d. in females.

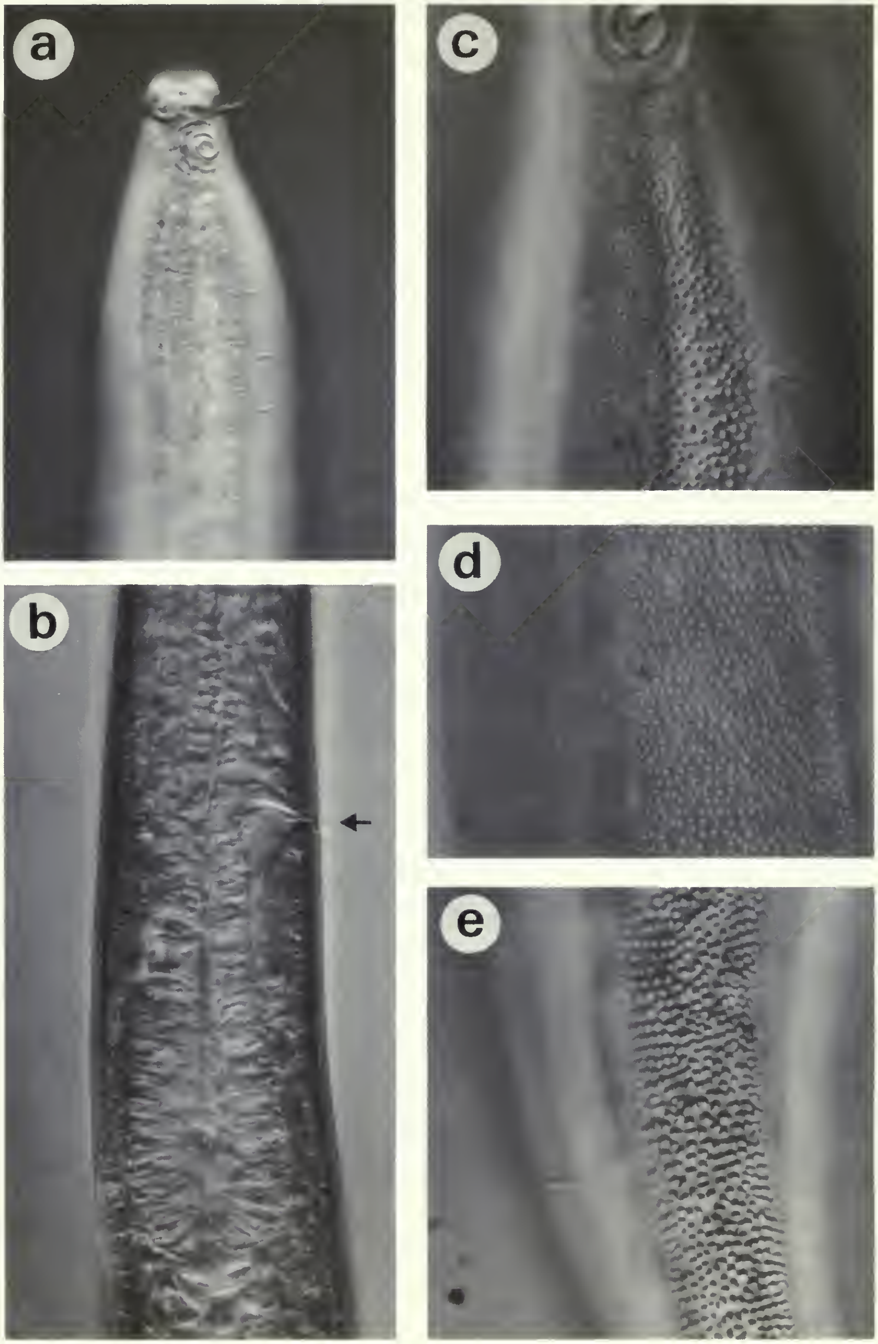


Fig. 3 *Sabatieria kelletti*: (a) anterior region showing row of three subventral cervical setae; (b) posterior oesophagus region showing excretory pore (arrowed) and posterior expansion of the oesophagus; (c) lateral cuticle pattern in post-amphid region; (d) lateral cuticle pattern mid-body; (e) lateral cuticle pattern on tail.

Table 1 Measurements of *Sabatieria kelletti* (μm)

Character	♂1	♂2	♂3	♂4	♂5	♂6	Mean	CV%	♀	J1	J2	J3	J4	J5
Total body length	3095	2700	2620	3020	2525	2775	2789	8·1	3295	2345	2270	2265	2210	1600
Demanian ratio a	36	40	31	39	37	36	37	8·6	35	38	34	36	33	36
Demanian ratio b	8·8	9·2	9·0	10·2	9·0	9·9	9·4	6·0	10·0	7·9	8·4	9·1	9·0	6·8
Demanian ratio c	12·4	11·5	12·8	13·1	11·5	13·4	12·5	6·5	12·7	10·7	10·8	11·2	11·1	9·7
R3 sensilla length	8	9	9	9	8·5	8	8·5	5·7	9·5	7·5	7·5	7·5	7·5	6·5
Head diameter	19	20	19	20	19	19	19	2·7	21	16	18	16	16	15
Amphid diameter	15	15	15	14	15	14	14·5	3·5	10	10	9	9·5	9·5	7·5
Amphid c.d.	24	22	22	22	22	23	22·5	3·7	26	17	20	19	19	17
Oesophagus length	350	295	290	295	280	280	298	8·8	330	295	270	250	245	235
Oesophagus c.d.	74	61	75	67	62	66	68	8·7	74	57	57	53	57	45
Maximum body diameter	87	68	85	78	69	78	78	10·2	95	62	67	63	67	45
Spicule length (chord)	63	60	63	62	64	60	62	2·7	—	—	—	—	—	—
a.b.d.	61	55	57	56	52	55	56	5·3	52	45	45	46	47	37
Cloaca to anterior supplement (*α*)	247	243	147	195	150	160	190	24·0	—	—	—	—	—	—
Cloaca to anterior supplement (*β*)	320	295	245	287	225	265	275	12·7	—	—	—	—	—	—
Number of supplements	27	24	22	23	22	21	—	—	—	—	—	—	—	—
Tail length	250	235	205	230	220	210	225	7·4	260	220	210	165	200	200

Spicules equal, curved; 1·0–1·2 a.b.d. as chord; 1·2–1·4 a.b.d. (68–72 µm) as arc. Gubernaculum with strongly curved apophyses which proximally are caudally directed. Ventral precloacal spine and 21–27 conspicuous precloacal supplements which extend 150–250 µm anterior to the cloaca measured along the ventral side of the body (measurement *α*) or 225–320 µm (9–11% of total body length) as measured along the mid-line of the body (measurement *β*). There is a very slight but distinct swelling resembling a flattened papilla between the conical and cylindrical parts of the male tail (Figs 1f, g, j & 2c, f) Two opposed testes: anterior to the left, posterior to the right of the gut.

Ovaries opposed and outstretched. Anterior ovary to the right, posterior to the left of the gut.

DIFFERENTIAL DIAGNOSIS. *Sabatieria kelletti* sp. nov. belongs to the *celtica*-group in terms of general body shape, cuticle punctation pattern, R3 sensilla length, amphid form and size, number of precloacal supplements and general tail shape. Indeed, the new species seems to be most similar to *S. celtica* Southern, 1914 itself, as redescribed by Lorenzen (1972), from which it differs in the range of supplement number (21–27 vs 15–22), more conspicuously narrowed and relatively smaller head (h.d. as percentage of posterior oesophagus c.d. 26–33% vs 33–42%), relatively shorter cephalic setae (0·4–0·5 h.d. vs 0·6–1·2 h.d.) and the presence in the male of a ventral caudal swelling or papilla.

ETYMOLOGY. The species is named after Mr Brian Kellett, my co-diver during the Antarctic peninsula collecting trip.

REMARKS. Because of the differing amounts of curvature in the posterior region of the males, measurement of the distance from cloaca to anteriormost supplement is subject to great variation (Table 1) even when an attempt is made to take into account the differing number of supplements among the specimens. For example, the ratio of the *α*-measurement to the number of supplements has a mean of 8·2 and a CV of 16·7%. However, this variation is less when the *β*-measurement is used, which should approximate the *α* of a straight worm: the ratio of *β* to supplement number has a mean of 11·8 and a CV of 7·8%. It would seem therefore that *β* would be the better measurement to report, although in view of the fact that *β* can be considerably larger than *α*, 1·2 to 1·7 times larger in *S. kelletti,* the exact method of measurement should also be reported.

Sabatieria lawsi sp. nov.

(Figs 4–6)

MATERIAL STUDIED. Holotype: ♂1 BM(NH) 1982.6.38. Allotype: ♀1 BM(NH) 1982.6.44. Paratypes: five males BM(NH) 1982.6.39–43; five females BM(NH) 1982.6.44–48; nineteen juveniles BM(NH) 1982.6.49–68.

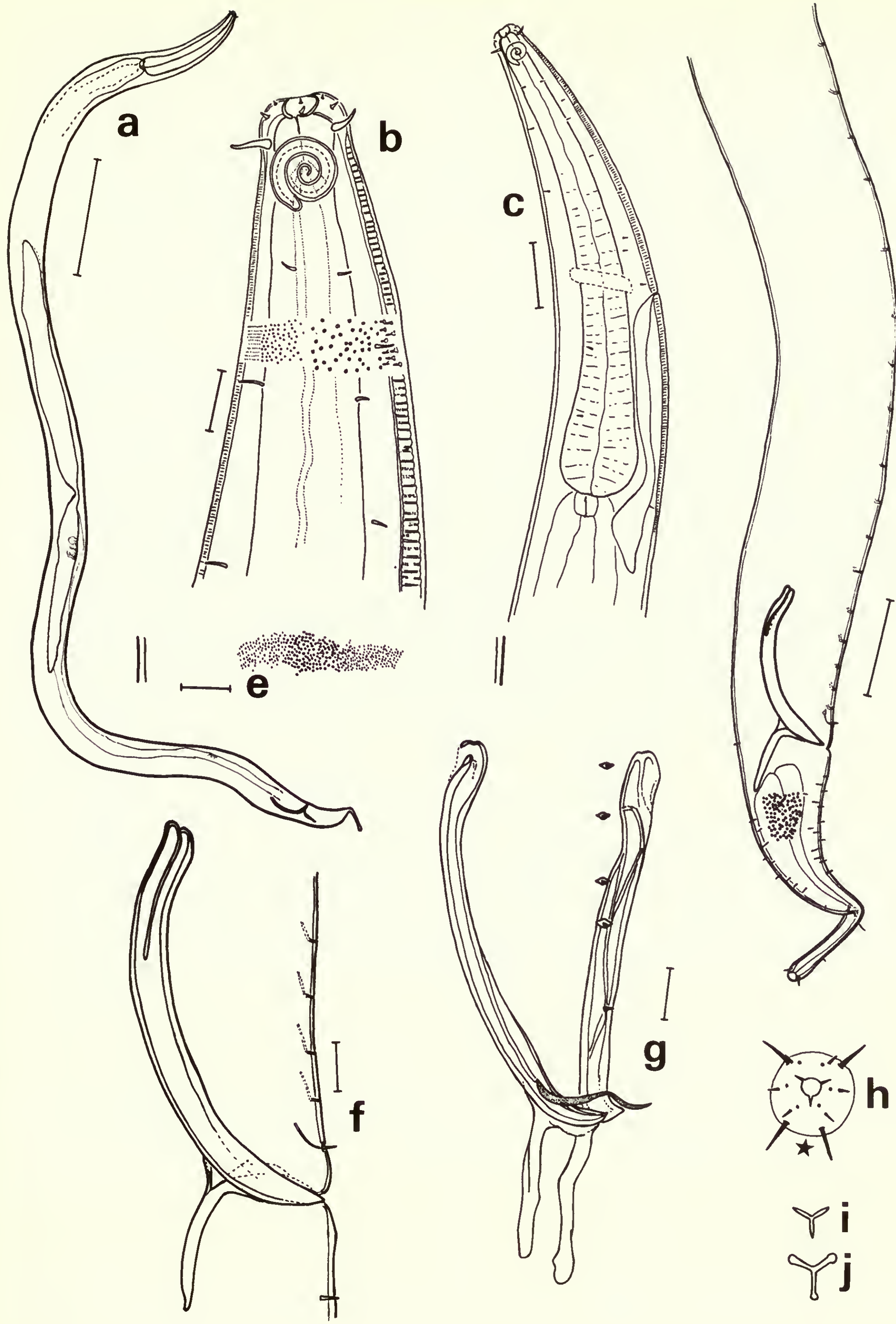
LOCALITY. See *S. kelletti.*

MEASUREMENTS (Tables 2 and 3)

Holotype ♂: $\dfrac{—\quad 233\quad \text{M}\quad 2250}{16\quad 57\quad 71\quad 46}$ 2400 µm; a = 34; b = 10·3; c = 16·2; S = 73 µm

Allotype ♀: $\dfrac{—\quad 233\quad 1180\quad 2395}{15\quad 52\quad 83\quad 50}$ 2595 µm; a = 31; b = 11·1; c = 12·9; V = 45%

Fig. 4 *Sabatieria lawsi*: (a) ♂1 whole body; (b) ♂1 head; (c) ♂1 anterior region; (d) ♂1 posterior region; (e) lateral cuticle pattern mid-body; (f) ♂1 copulatory apparatus; (g) ♂ copulatory apparatus, ventral view; (h) en face view; (i) buccal cavity lumen shape level with R3 sensilla; (j) oesophagus lumen shape just posterior to amphids. Bar scales: a = 200 µm; d = 50 µm; c = 30 µm; others = 10 µm. Star in h indicates the ventral side.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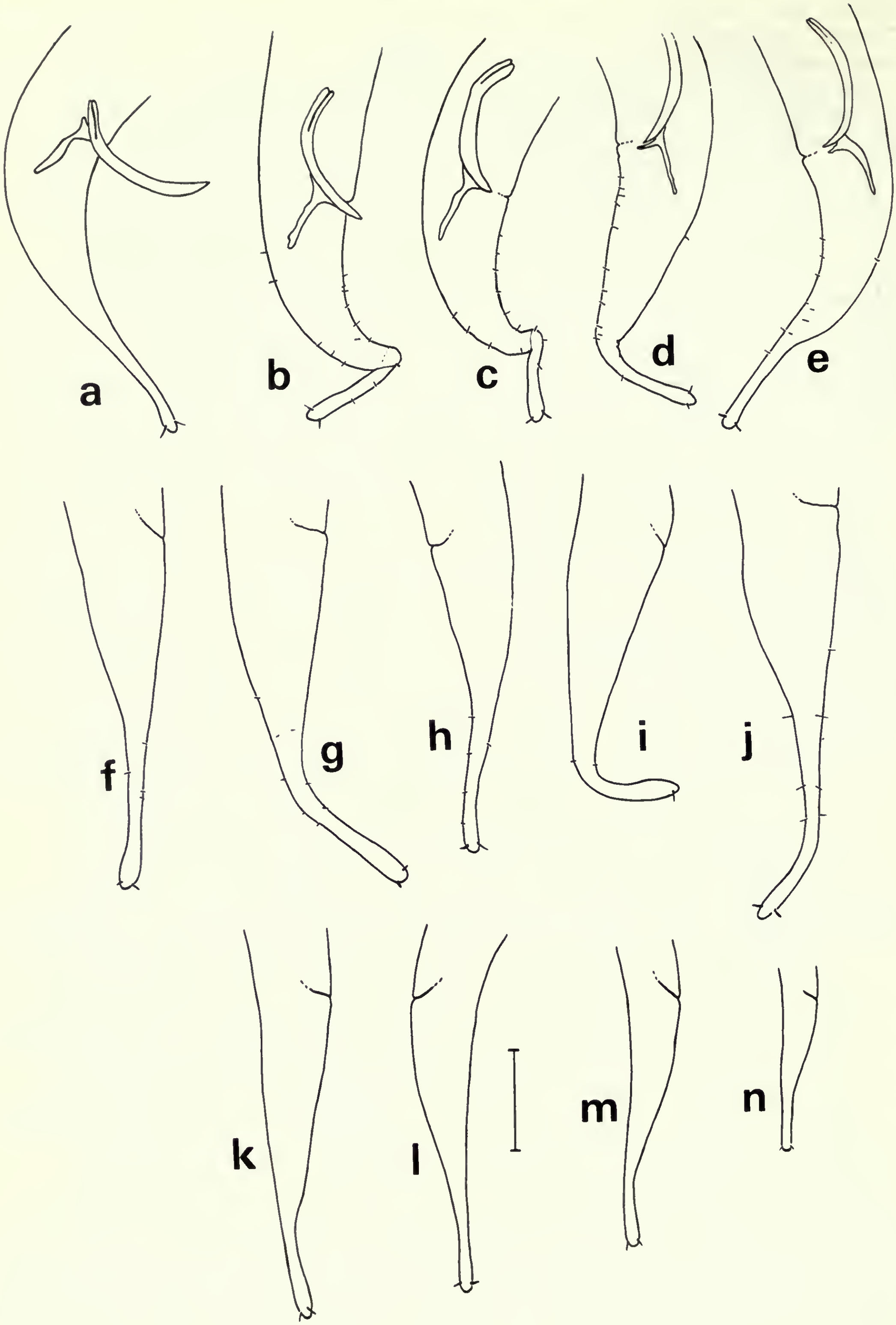
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Description. The anterior region gradually narrows from the end of the oesophagus to the head: h.d. 26–35% of the posterior oesophagus c.d. The anterior end is typically bent dorsally in formalin-fixed specimens (Fig. 4c).. Cuticle punctated. Lateral differentiation of larger, more irregularly arranged dots begins immediately posterior to the amphids and is especially conspicuous in the oesophageal and caudal regions. In the middle region of the body the lateral dots are not so markedly larger than the medial ones but they are still more irregularly arranged (Fig. 6c). The decrease in the size of the lateral dots posterior to the oesophagus region occurs gradually. In the anterior oesophagus, the dots appear somewhat stellate when the microscope is focused at the surface (Fig. 6b). The dots are also conspicuously large ventrally in the oesophagus region (Fig. 4b, c). Short but stout somatic setae are located at the edges of the lateral field, relatively more numerous in the oesophagus and tail regions where there are also some subdorsal and subventral somatic setae: no regular repeated or distinctive patterns could be made out in the distribution of somatic sensilla. R1 sensilla papilliform but conspicuous. R2 sensilla very short but setiform, about 1·5 µm (Fig. 6a). R3 sensilla 32–44% h.d.: similar relative length in juveniles. Amphids in adults describe almost 3 turns (Fig. 6a); similar in size in both sexes, 48–66% c.d. Buccal cavity cup-shaped anteriorly, posterior part tubular and tri-radiate (Fig. 4i) but not expanded. Oesophagus widens posteriorly: marginal tubes at the ends of the radii can be seen in optical cross-section (Fig. 4j). Nerve ring at 50–54% of oesophagus length. Excretory pore at 53–66% of oesophagus length. Tail conico-cylindrical with the cylindrical part about 33% of the total which shows little variation (Fig. 5): 3·1–3·8 a.b.d. in males, 3·8–4·6 a.b.d. in females. There appear to be separate subterminal openings to the caudal glands at the tail tip (Fig. 6f, g).

Spicules equal, curved, relatively long and slender with a proximal median partition extending up to a third of the total spicule length (Fig. 4f): 1·6–1·7 a.b.d. (chord). Gubernaculum apophyses long, straight and dorso-caudally directed. Ventral view of cloacal opening shows it to be a double-bowed transverse slit (Fig. 4g). Ventral precloacal spine about 1·5 µm (Fig. 6h). 17 inconspicuous tubular precloacal supplements extending 355–385 µm from cloaca (β) or 15–17% of total body length. The posterior 4 or 5 supplements are situated closer together than the remainder. Two opposed testes; anterior to left, posterior to right of gut.

Ovaries opposed, outstretched. Vulva conspicuous; V = 45–49%. Eggs round. Receptaculum seminis of mature females contain large hollow sperm (Fig. 6d, e).

Differential diagnosis. *Sabatieria lawsi* sp. nov. belongs to the *celtica*-group of species in terms of general body shape, cuticle punctation pattern, R3 sensilla length, amphid form and size, number of precloacal supplements and general tail shape. In several respects, the new species appears to be similar to *S. heterura* (Cobb, 1898), a species originally found in Australia and subsequently redescribed by Wieser (1954) on specimens from Chile. However, the species may be distinguished most easily by the detailed structure of the spicules and gubernaculum.

Etymology. The species is named after Dr R. M. Laws, Director of the British Antarctic Survey.

Remarks. *Sabatieria lawsi* would appear to be the more common of the sympatric *Sabatieria* species: they could be readily distinguished even in the juvenile stages by the markedly different shape of the oesophagus region.

The hollow sperm in the females were similar to those previously reported from *Sabatieria* by Riemann (1983).

Fig. 5 *Sabatieria lawsi:* (a–e) tails of ♂5, ♂6, ♂4, ♂2 and ♂3, respectively; (f–j) tails of ♀5, ♀1, ♀4, ♀3 and ♀2 respectively; (k–l) tails of fourth-stage J1 and J4; (m) tail of third-stage J7; (n) tail of second-stage J15. Bar scale = 50 µm for all figures.

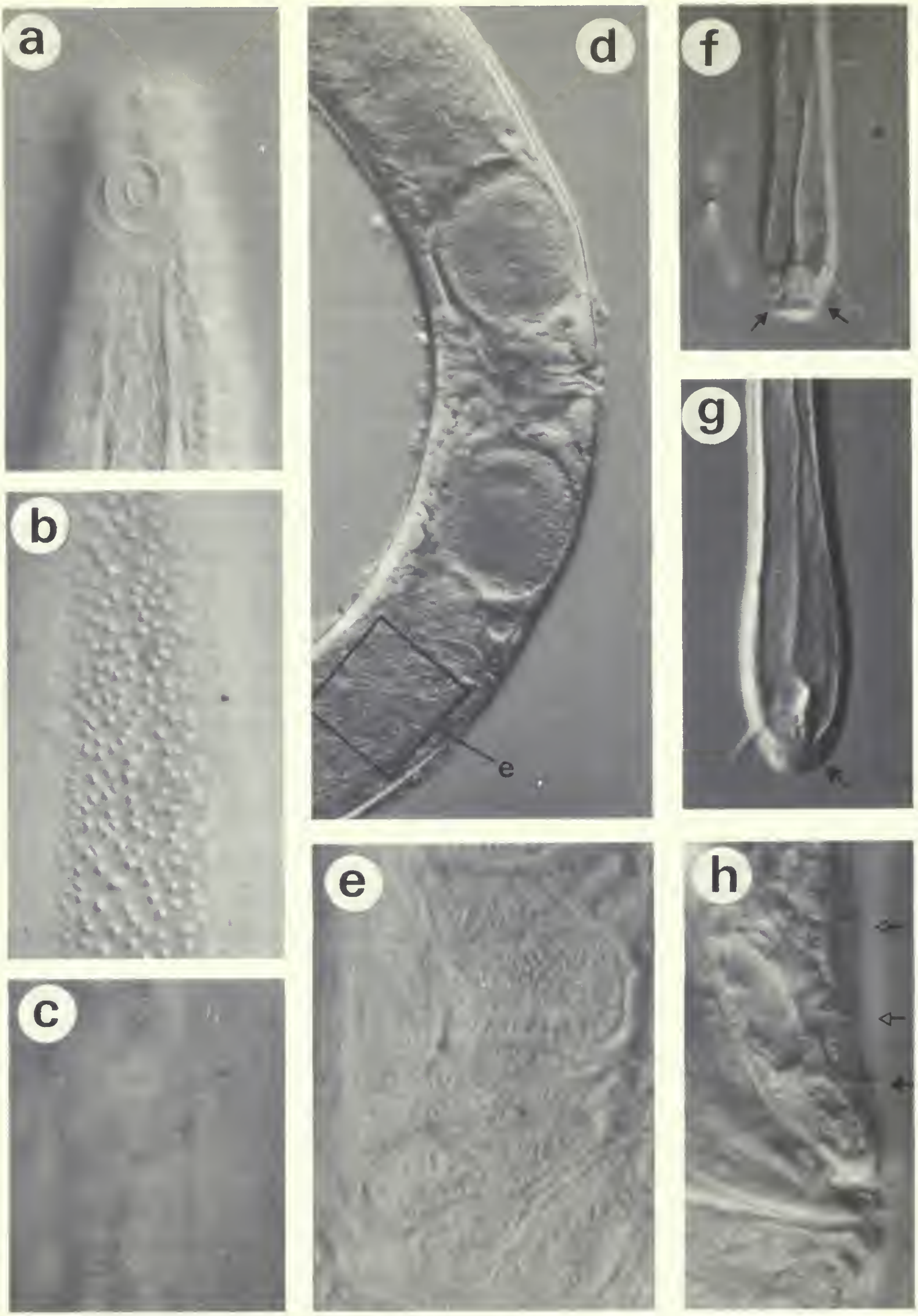

Fig. 6 *Sabatieria lawsi:* (a) anterior region showing amphid, R3 sensilla and lateral R2 sensilla; (b) lateral cuticle punctations in post-amphid region; (c) lateral cuticle pattern mid-body; (d) mid-body region of ♀ showing vulva and two eggs, box labelled e shows position of following figure; (e) large hollow sperm in receptaculum seminis, see Fig. 6d; (f–g) tail tips showing exit pores of caudal glands, arrowed; (h) precloacal region showing spine (solid arrow) and first two supplements (hollow arrows).

Table 2 Measurements of adult *Sabatieria lawsi* (μm)

Character	Holotype	All males				Allotype	All females			
		No.	Mean	Range	CV%		No.	Mean	Range	CV%
Total body length	2400	6	2250	2060–2400	6	2595	6	2295	1940–2595	12
Demanian ratio a	34	6	34	32–35	4	31	6	31	26–34	8
Demanian ratio b	10·3	6	10·0	8·8–10·6	7	11·1	6	9·8	8·4–11·1	12
Demanian ratio c	16·2	6	14·5	12·0–16·2	11	12·9	6	12·3	11·7–13·3	6
R3 sensilla length	6	6	6	6–7	10	7	6	6	5–7	10
Head diameter	16	6	15	14–16	4	15	5	16	15–18	6
Amphid diameter	11	6	10	9–11	7	10	6	10	8–10	12
Amphid c.d.	16	6	18	16–19	5	19	6	17	16–19	6
Oesophagus length	233	6	225	201–235	6	233	6	236	226–243	3
Oesophagus c.d.	57	4	56	54–57	3	52	6	55	47–62	9
Maximum body diameter	71	6	67	61–74	7	83	6	76	57–95	17
Spicule length (chord)	73	6	73	70–75	—	—	—	—	—	—
a.b.d.	46	6	44	43–46	2	50	6	45	39–50	10
Vulva to anterior	—	—	—	—	—	1180	6	1065	950–1180	9
Cloaca to anaterior supplement (*β*)	355	4	363	340–385	5	—	—	—	—	—
Tail length	150	6	155	135–170	9	200	6	185	165–215	10

Table 3 Measurements of juvenile *Sabatieria lawsi* (μm)

Character	Fourth-stage juveniles				Third-stage juveniles				Second-stage juveniles			
	No.	Mean	Range	CV%	No.	Mean	Range	CV%	No.	Mean	Range	CV%
Total body length	4	1705	1585–1860	7	6	1130	1025–1295	8	9	725	630–850	9
Demanian ratio a	4	31	29–35	8	6	29	26–32	10	9	27	24–30	7
Demanian ratio b	4	8·2	7·9–8·4	3	6	6·8	6·5–7·1	3	9	5·1	4·7–5·8	7
Demanian ratio c	4	11·2	10·5–12·7	9	6	9·7	8·3–10·7	12	9	8·5	7·8–9·3	6
R3 sensilla length	4	5·2	4·4–5·9	12	6	4·8	4·4–5·2	7	8	4·2	3·7–4·8	10
Head diameter	4	13	11–15	12	5	11	9–13	13	7	9	7–11	11
Amphid diameter	4	8	7–8	5	5	7	6–8	10	8	5	4–6	19
Amphid c.d.	4	14	13–16	10	5	13	11–14	11	8	11	9–13	11
Oesophagus length	4	208	192–225	7	6	166	144–187	9	9	142	124–182	12
Maximum body diameter	4	55	53–56	2	6	39	36–41	6	9	27	24–32	9
Tail length	4	155	130–170	11	6	115	100–130	9	9	85	75–105	12

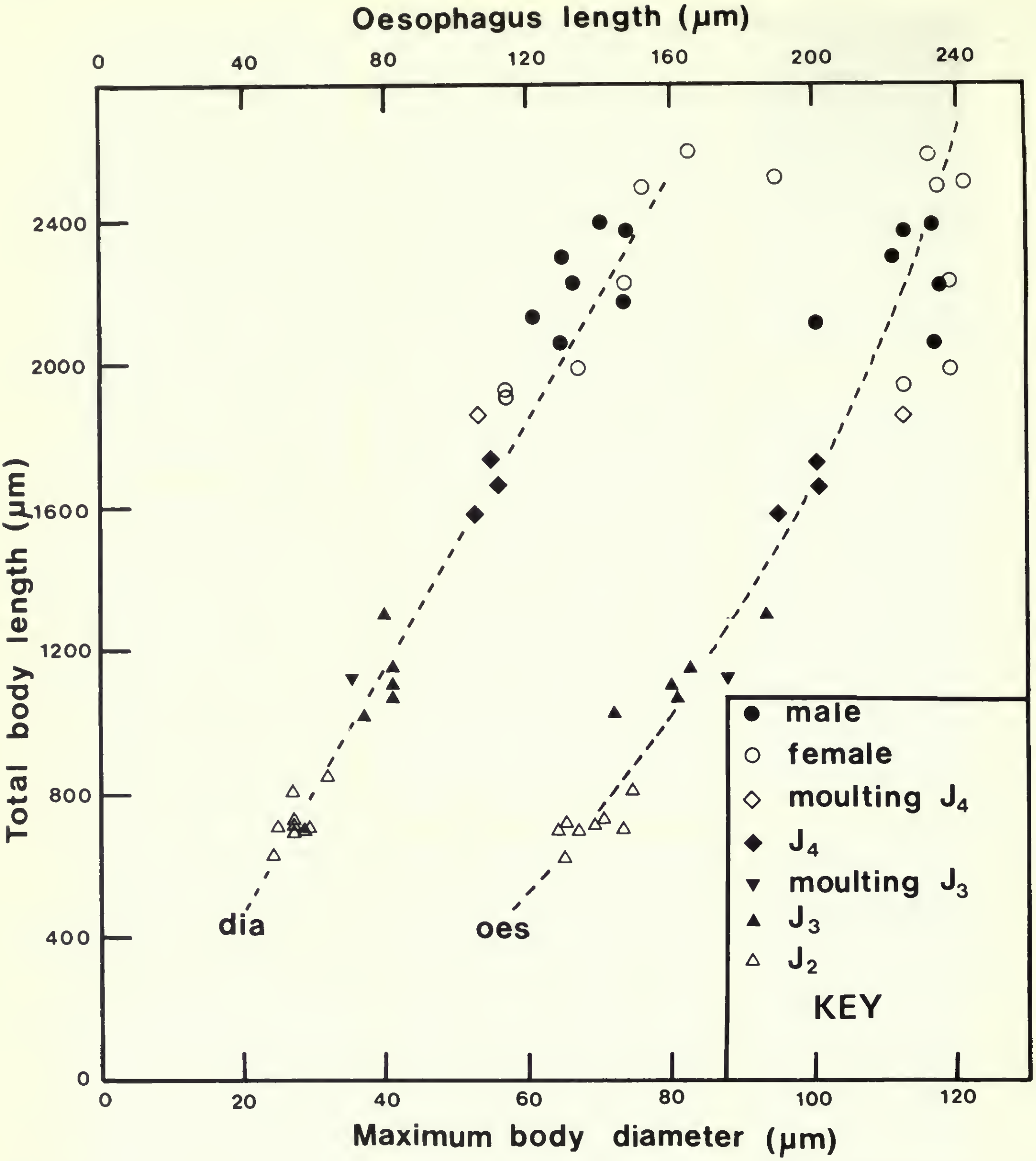

Fig. 7 Relationships between body length and oesophagus length, and body length and maximum body diameter for *S. lawsi*: curves fitted by eye.

Discussion

Although several species of *Sabatieria* have previously been reported from Antarctic waters (as defined in Platt, 1979) only one can be considered valid: *Sabatieria mawsoni* Wieser, 1954 which was originally described from Commonwealth Bay, Adelie Land, as *Parasabatieria antarctica* by Cobb (1930). Cobb provided a small and rather inadequate figure but described it as having six supplements, which clearly separates it from the two species described here. *Sabatieria antarctica* Cobb, 1914, not *Parasabatieria antarctica*, was described from a juvenile and was considered doubtful by Wieser (1954). Allgen's (1929)

S. australis was also described from juveniles and is here considered dubious as are several other species either described, *S. curvispiculum, S. dorylaimopsis* and *S. heterospiculum*: all from South Georgia and unfortunately too poorly described ever to be recognised again with any degree of certainty, or reported from Antarctic waters by Allgen (1953, 1959).

Measurements of *S. lawsi* juveniles and adults suggest that during post-embryonic growth, or more strictly during post-juvenile-stage-4 growth, most of the anatomical features other than those of the reproductive system remain in similar proportion. There is some indication from the 'a' ratio that the worms become slightly thinner relatively (Tables 2 & 3) although a straight line can be fitted to the points of the relationship between body length and width (Fig. 7); that this line does not pass through the origin suggests a curved line might be more appropriate. Geraert (1978*a*, 1979*a*) also concluded that various freeliving soil forms became relatively thinner during post-embryological growth but became thicker again during maturation.

A less equivocal change can be seen in the relative length of the oesophagus, with the 'b' ratio increasing (i.e. the oesophagus becoming relatively shorter) with no overlap in the ranges for the various developmental stages, assuming these have been correctly identified (Tables 2 and 3). Geraert (1978*a*, 1978*b*, 1979*a*) found that for freeliving soil forms there were many different kinds of oesophageal growth patterns: the shape of the curve in Fig. 7 suggests that for *S. lawsi* the oesophagus continues to grow in all stages but progressively slows down, as Geraert found occurred in rhabditids.

In his study of relative tail length, Geraert (1979*b*) concluded that the 'c' ratio was of minor importance and that tail length varied independantly and was taxonomically unimportant. However, the relatively low CV for these measurements in marine nematodes together with low infraspecific variability in shape (Fig. 5) indicates that at least for these comesomatids, characters of the tail are of greater importance than in the soil forms studied by Geraert, possibly because in marine nematodes the tail plays a greater functional role than in soil forms.

A final point of interest to emerge from this study is the general range of infraspecific variation found in these organisms in view of what would appear to be very stable and cold environmental temperatures. The CV for most characters was under 10% (Tables 1–3), similar to but not any less than the range previously reported for *Sabatieria* species from warmer waters (Jensen & Gerlach, 1977; Jensen, 1979*a*, 1979*b*). The maximum body diameter CV can exceed 10%, especially in females (Table 2) but this, as pointed out by Jensen (1979*a*) is influenced by the state of gonad development.

Acknowledgements

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New species of marine nematodes from Qingdao, China

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Introduction

This paper is the first taxonomic report on freeliving marine nematodes from China. The three new oncholaimid species described here were extracted from intertidal sand samples taken from beaches adjacent to the city of Qingdao in summer, 1981.

Material and methods

The specimens came from two intertidal localities: mid-tide level on Qingdao bathing beach and mean low water level east of Qingdao pier. Cumulative curves of the sediment grain size analysis data are shown in Fig. 1. The pier beach is considered polluted by sewage whereas the bathing beach is relatively clean. Methods of microscopic study, abbreviations and style of description were as set out in Platt & Zhang (1982).

Systematic descriptions

Oncholaimus qingdaoensis sp. nov.

Fig. 2

MATERIAL STUDIED. Holotype: ♂$_1$ BM(NH) 1982.1.2. Allotype: ♀ BM(NH) 1982.1.5. Paratypes: two males BM(NH) 1982.1.3–4.

LOCALITY. Qingdao bathing beach, Shandong, China.

DIMENSIONS

♂$_1$: $\frac{-\quad 372\quad \mathrm{M}\quad 2590}{20\quad 25\quad 27\quad 20}$ 2640 µm; a=98; b=7; c=53

♂$_2$: $\frac{-\quad 384\quad \mathrm{M}\quad 2370}{22\quad 21\quad 25\quad 21}$ 2420 µm; a=97; b=6; c=48

♂$_3$: $\frac{-\quad 340\quad \mathrm{M}\quad 2331}{20\quad 21\quad 26\quad 20}$ 2380 µm; a=92; b=7; c=49

♀: $\frac{-\quad 365\quad \mathrm{M}\quad 2300}{22\quad 31\quad 32\quad 24}$ 2350 µm; a=73; b=6; c=47

DESCRIPTION. Cuticle smooth. R_1 sensilla papilliform. R_2+R_3 sensilla at the same level and equal in size: 8–9 µm, 40–45% h.d. Head constricted immediately posterior to cephalic setae. Amphid 9 µm wide, 40% c.d.: in some individuals the amphids are difficult to distinguish. Buccal cavity 25–27 µm deep. Large left subventral, small right subventral and small dorsal

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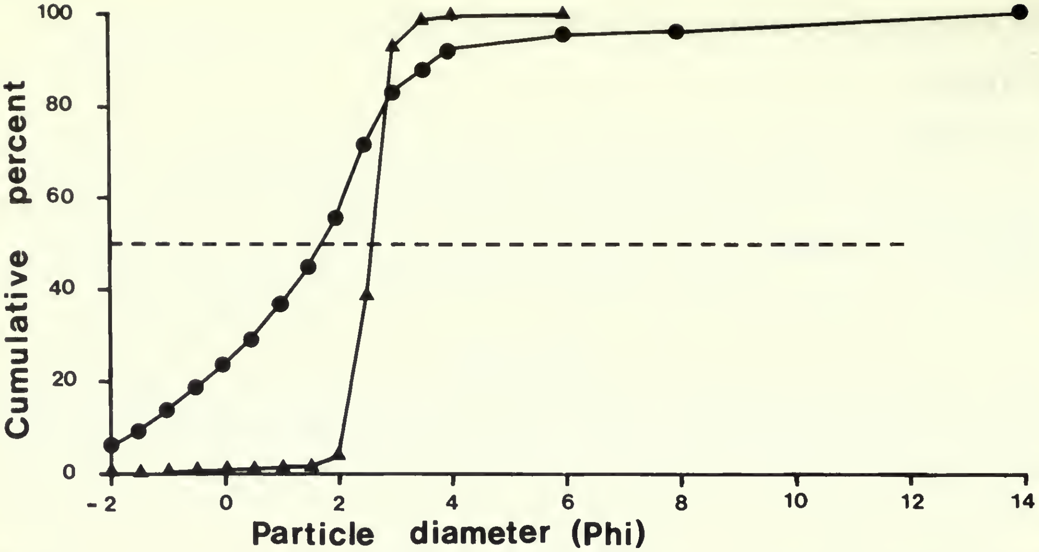

Fig. 1 Cumulative curves from the sediment analysis data for: (▲—▲) Qingdao bathing beach; (●—●) Qingdao pier beach sediments.

teeth. Oesophagus without bulb. Excretory pore situated 48–64 μm from the anterior, about 2–2·5 times the length of the buccal cavity (Fig. 2a, b). Nerve ring situated at 43–48% of oesophagus length. Tail conical, slightly curved ventrally; 2·0 a.b.d. in female, 2·5 a.b.d. in male.

Spicules equal, 34–36 μm (1·8 a.b.d.), proximally cephalate and pointed distally. Gubernaculum absent. Pairs of 3–7 μm special subventral stout spine-like setae: 4 pairs precloacal, 4 pairs adcloacal and 3 pairs on the tail. Two pairs of precloacal spines, not conspicuously situated on papillae. Conspicuous ventral papilla about 12 μm from the tail tip (Fig. 2c, d). Two opposed testes.

Vulva at 69% of total length. Single anterior ovary. A demanian system could not be distinguished in the only female available for study.

DIFFERENTIAL DIAGNOSIS. *Oncholaimus qingdaoensis* sp. nov. belongs to a group of species which have a conspicuous papilla near the male tail tip. Of these species, in terms of tail shape, the new species most closely resembles *O. cobbi* (Kreis, 1932), *O. domesticus* (Chitwood & Chitwood, 1938), *O. hyrcanus* Tchesunov, 1979 and *O. longus* (Wieser, 1953). Amongst several minor differences, *O. qingdaoensis* may be differentiated from *O. longus* by its less slender body (male a = 92–98 vs 130–150) and more anterior excretory pore (2–2·5 vs 4 buccal cavity lengths from anterior); from *O. cobbi* by the fewer number of adcloacal pairs of spines (4 vs 10–15), shape of the postcloacal papilla and the presence of precloacal spines; from *O. domesticus* by the lack of a well-developed demanian system with adanal or postanal openings; from *O. hyrcanus* by the lack of unequal spicules, lack of conspicuous precloacal papilla and different shape of the female tail. In addition, *O. qingdaoensis* appears to differ from all of these four species in having its larger left subventral tooth more conspicuously anterior to the dorsal and right subventral teeth.

ETYMOLOGY. The species name refers to the city near the type locality.

DISCUSSION. The genus *Oncholaimus* Dujardin, 1845 and the related genera are currently in some considerable state of confusion and badly need revising. Several sets of *Oncholaimus*-like species have been placed in separate genera, the bases of which appear to be breaking down in the light of more recent findings. Genera separated from *Oncholaimus* include *Metaparoncholaimus* De Coninck & Stekhoven, 1933 on the presence of two large

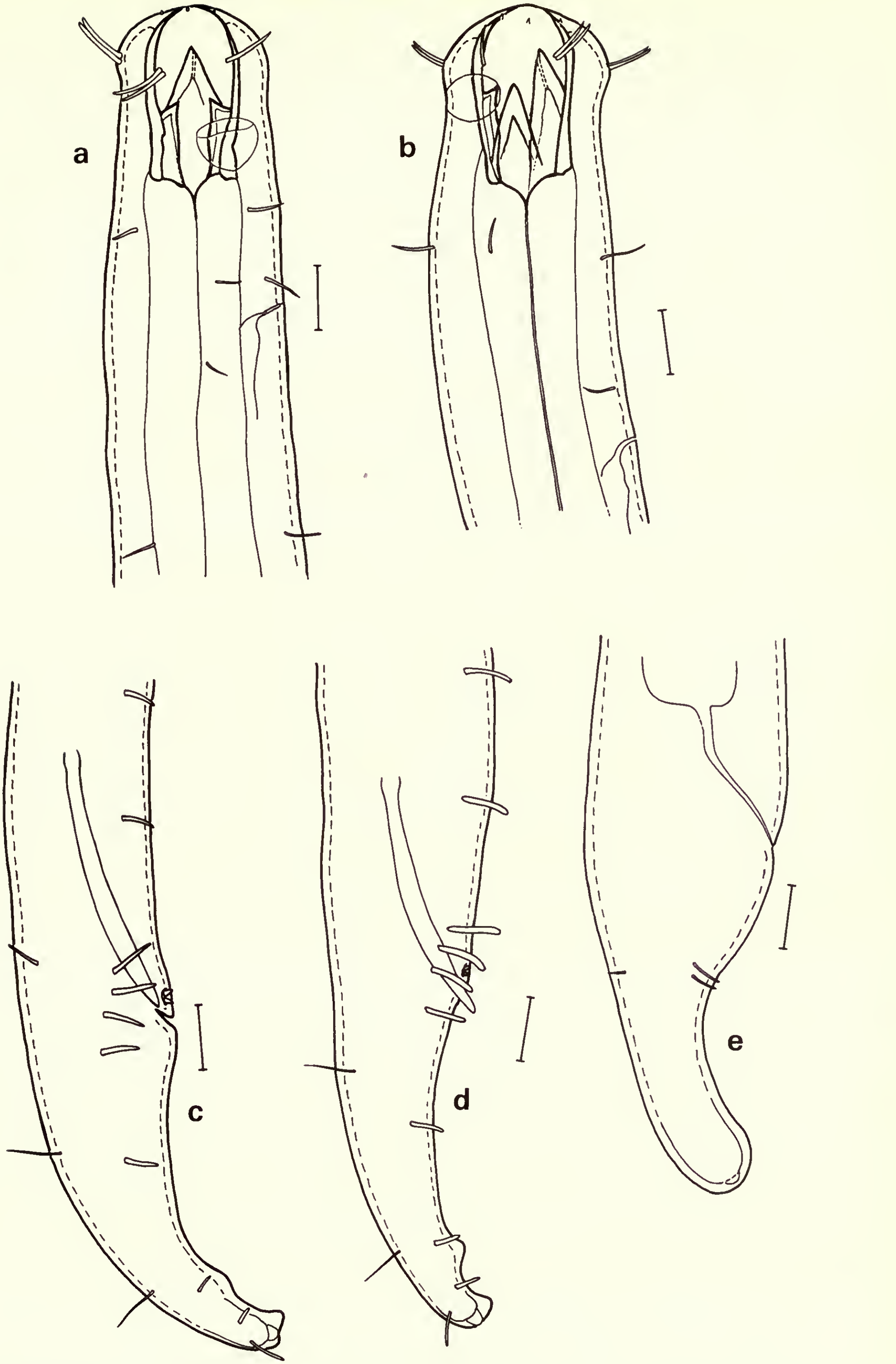

Fig. 2 *Oncholaimus qingdaoensis*: (a) ♂$_1$ head; (b) ♂$_2$ head; (c) ♂$_1$ tail region; (d) ♂$_3$ tail region: (e) ♀ tail region. Bar scales: 10 μm,

equal subventral teeth; *Oncholaimium* Cobb, 1930 on (originally) the presence of a precloacal papilla and a demanian system without exit pores; *Pseudoncholaimus* Kreis, 1932 on the absence of a demanian system. Rachor (1969) considered the last two to be synonymous with *Oncholaimus.* So, for the purposes of this analysis, species previously assigned to *Oncholaimium* and *Pseudoncholaimus* have been considered along with *Oncholaimus* sensu stricto. Altogether, this group includes 91 known species, of which 26 are considered to be dubious on the grounds of inadequate description.

Several *Oncholaimus* species have been reported as having teeth of equal or almost of equal length, e.g. *O. nigrocephalatus* Cobb, 1930, *O. opisthonchus* Filipjev, 1927 and *O. problematicus* Coles, 1977. Indeed, drawings of these species differ little from De Man's original (1876) drawing of *Metaparoncholaimus campylocercus*, the genotype. Therefore, any future revision of this group should carefully consider whether *Metparoncholaimus* should be maintained as a distinct genus or whether the relative tooth sizes should be considered a variable infrageneric character within *Oncholaimus*, albeit of great use in practical identification.

Oncholaimus sinensis sp. nov.

Fig. 3

Material studied. Holotype: ♂$_1$ BM(NH) 1982.1.6. Paratypes: ♂$_2$ BM(NH) 1982.1.6, ♂$_3$ in the collection of Z. N. Zhang and one juvenile BM(NH) 1982.1.7.

Locality. East of Qingdao pier, Shandong, China.

Dimensions

♂$_1$: $\dfrac{—\quad 310\quad M\quad 1990}{19\quad 38\quad 40\quad 22}$ 2080 µm: $a=52$; $b=7$; $c=23$

♂$_2$: $\dfrac{—\quad 325\quad M\quad 1930}{20\quad 39\quad 40\quad 23}$ 2010 µm; $a=50$; $b=6$; $c=25$

♂$_3$: $\dfrac{—\quad 340\quad M\quad 2074}{22\quad 40\quad 42\quad 23}$ 2160 µm; $a=51$; $b=6$; $c=25$

Juvenile: $\dfrac{—\quad 405\quad M\quad 2480}{21\quad 35\quad 35\quad 23}$ 2570 µm; $a=73$; $b=6$; $c=29$

Description. Cuticle smooth. R$_1$ sensilla papilliform. R$_2$+R$_3$ sensilla at the same level and almost the same length: 5–6·5 µm, 25–33% h.d. Amphid 7 µm wide, 29% c.d., situated just anterior to dorsal tooth. Buccal cavity 24–26 µm deep, armed with large left subventral tooth and smaller right subventral and dorsal teeth. Excretory pore situated 80–93 µm from anterior, about 3 times the length of the buccal cavity (Fig. 3a). Nerve ring situated at 45–51% of oesophagus length. Tail conico-cylindrical, 3·5–4 a.b.d. with slightly swollen tip.

Spicules equal, 26–27 µm (1·2 a.b.d.), proximally slightly cephalate, distally pointed but with some striations on the ventral side. Gubernaculum absent. Relatively conspicuous 'fleshy' precloacal papilla present. There is also a ventral postcloacal papilla situated at about 60% of the tail length from the cloaca with two pairs of 3 µm setae. About 11 pairs of 4·5–7 µm adcloacal setae in addition to subdorsal caudal setae.

Differential diagnosis. *Oncholaimus sinensis* sp. nov. most closely resembles *O. appendiculatus* (Cobb, 1930) and *O. campylocercoides* De Coninck & Stekhoven, 1933 in the presence of a prominent precloacal papilla and a conico-cylindrical tail. However, *O. campylocercoides* as originally described and as redescribed by Gerlach (1952) apparently lacks the postcloacal papilla, although Wieser (1959) mentions and figures the presence of *two* setose papillae in the middle of the tail. *O. appendiculatus* has a single ventral postcloacal papilla but the spicules are much longer than those of the new species. Three other species

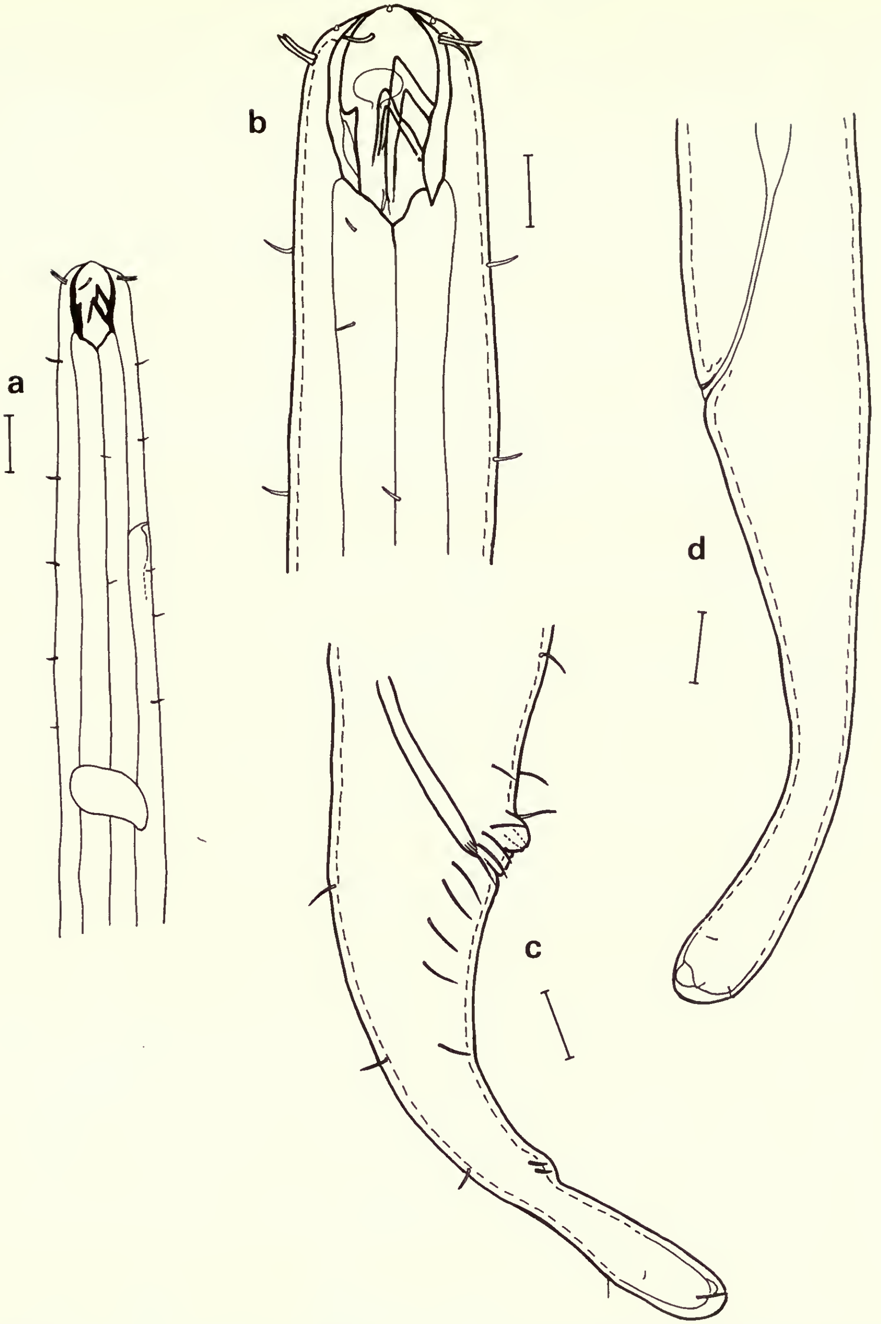

Fig. 3 *Oncholaimus sinensis*: (a) ♂$_1$ anterior region; (b) ♂$_1$ head; (c) ♂$_1$ tail region; (d) juvenile tail region. Bar scales: a = 20 µm; b–d = 10 µm.

have been described with single postcloacal papillae and similarly shaped tails, *O. manilius* Gerlach, 1957, *O. martini* Wieser, 1959 and *O. olium* Belogurov, Belogurova & Pavluk, 1975: all lack the conspicuous precloacal supplement and have their amphids situated more posteriorly than in *O. sinensis.*

Etymology. The species name refers to the country of the type locality.

Discussion. It is hoped that an analysis of the female demanian system will be given in the near future when new material is available. In the meantime, the assessment of these Chinese specimens as belonging to a distinct species rests on the male characters alone. Judging from descriptions in the literature, and in view of the need for a revision of the genus as discussed above, it is considered that there are sufficient minor points of difference between *O. sinensis* males and those of species which most closely resemble them to support the Chinese species as being new. In any event, to place them in an already extant species would be to risk submerging what might be useful information. The striated nature of the tip of the spicule, for example, does not appear to have been reported hitherto, but may possibly have been overlooked in some other species.

Metoncholaimus moles sp. nov.

Fig. 4

Material studied. Holotype: ♂$_1$ BM(NH) 1982.1.8. Allotype: ♀$_1$ BM(NH) 1982.1.9. Paratypes: two males BM(NH) 1982.1.8. and two females BM(NH) 1982.1.9.

Locality. East of Qingdao pier, Shandong, China.

Dimensions

♂$_1$: $\frac{—\quad 420\quad \mathrm{M}\quad 3172}{25\quad 52\quad 52\quad 35}$ 3320 µm; a = 64; b = 8; c = 22

♂$_2$: $\frac{—\quad 420\quad \mathrm{M}\quad 3540}{25\quad 54\quad 55\quad 39}$ 3700 µm; a = 67; b = 9; c = 23

♂$_3$: $\frac{—\quad 446\quad \mathrm{M}\quad 3292}{24\quad 54\quad 54\quad 38}$ 3440 µm; a = 64; b = 8; c = 23

♀$_1$: $\frac{—\quad 440\quad \mathrm{M}\quad 2820}{24\quad 53\quad 53\quad 36}$ 2950 µm; a = 56; b = 7; c = 23

♀$_2$: $\frac{—\quad 450\quad \mathrm{M}\quad 3685}{24\quad 59\quad 61\quad 36}$ 3820 µm; a = 63; b = 9; c = 28

♀$_3$: $\frac{—\quad 440\quad \mathrm{M}\quad 3204}{27\quad 57\quad 58\quad 36}$ 3340 µm; a = 58; b = 8; c = 25

Description. Cuticle smooth. Six papilliform R_1 sensilla. $R_2 + R_3$ sensilla at the same level: R_2 sensilla 7–8 µm, 28–32% h.d.; R_3 sensilla 5–7·5 µm, 20–30% h.d. Somatic setae 5–7 µm, most numerous in the anterior oesophageal region. Head somewhat attenuated. Amphid usually distinct, 10 µm wide (33% c.d.) and situated level with the dorsal tooth. Buccal cavity 26–30 µm deep. Large left subventral tooth and smaller right subventral and dorsal teeth. Oesophagus widens slightly towards the posterior, but no bulb. Excretory pore just posterior to the base of the buccal cavity, 29–36 µm from the anterior. Nerve ring at 44–49% of the oesophagus length. Tail conico-cylindrical, 3·6–4·2 a.b.d. with a characteristic ventral inflection of the tip in the male (Fig. 4d).

Spicules equal, 43–44 µm (chord), proximally cephalate and distally pointed (Fig. 4e). Gubernaculum present with a well-developed dorsally directed apophysis, 21–22 µm long. There are 9–11 pairs of stout adcloacal setae. Precloacally, there are an additional 4–6 thicker but shorter setae (Fig. 4e): a further 3 pairs of similar setae are found subventrally near the tail tip (Fig. 4f). Two testes.

Vulva situated posterior to the mid-body; V = 68–78%. Single anterior ovary. Demanian system appears to be relatively simple, typical of other *Metoncholaimus* species (Rachor, 1969). The terminal duct opens as a transverse slit about 65 µm anterior to the anus. The body is constricted immediately posterior to the pore (Fig. 4g), and in this region there are characteristic subdorsal and subventral pairs of setae.

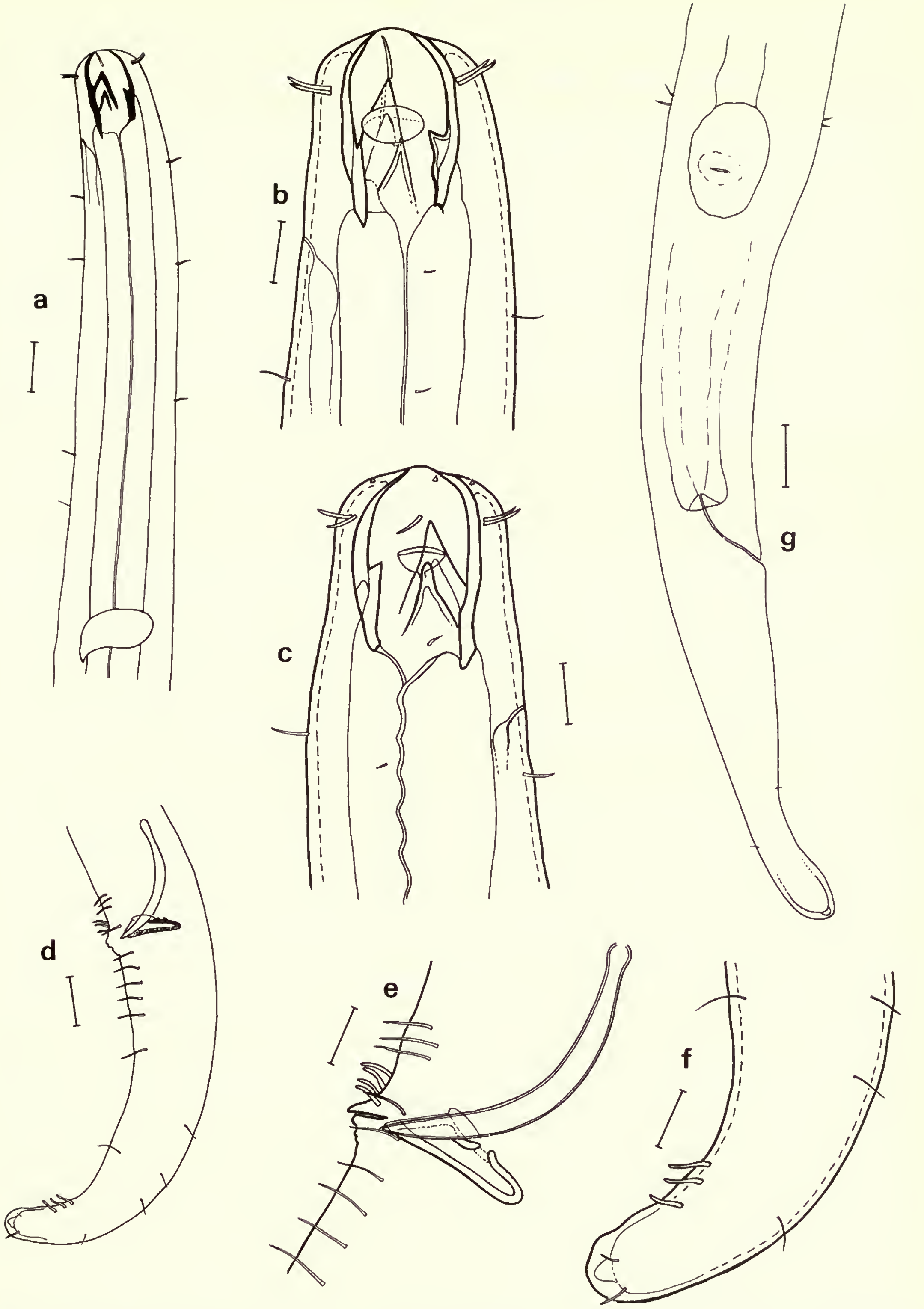

Fig. 4 *Metoncholaimus moles*: (a) ♂$_1$ anterior region; (b) ♂$_1$ anterior region; (c) ♀$_1$ head region; (d) ♂$_1$ tail region; (e) ♂$_1$ copulatory apparatus; (f) ♂$_1$ tail tip; (g) ♀$_1$ posterior region. Bar scales: a, d, g = 20 μm; b, c, d, e = 10 μm.

DIFFERENTIAL DIAGNOSIS. *Metoncholaimus moles* sp. nov. is unique among the thirteen previously described species in having a well-developed dorsally directed gubernaculum.

ETYMOLOGY. The species name refers to the type locality being near a pier (moles, Latin = pier).

DISCUSSION. The traditional distinction between the genera *Oncholaimus* Dujardin, 1845 and *Metoncholaimus* Filipjev, 1918 is another that is beginning to break down. Characteristically, *Oncholaimus* species have short spicules and no gubernaculum whilst *Metoncholaimus* species have extremely long spicules and a small gubernaculum lying parallel with the distal end of the spicules, e.g. *M. demani* Zur Strassen. Already a number of *Oncholaimus* species have been described with simple gubernacula, e.g. *O. gladius* Gerlach, 1956, *O. longispiculosus* Gerlach, 1955 and *O. dujardini* sensu Wieser, 1953. *Metoncholaimus* species with long spicules but without a gubernaculum have also been reported, e.g. *M. intermedius* Wieser & Hopper, 1967 and *M. scissus* Wieser & Hopper, 1967. However, none of the *Oncholaimus* or *Metoncholaimus* species, nor any species belonging to other genera of the Oncholaiminae, have, to the best of our knowledge, been described as having a dorsally directed gubernaculum.

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Echinoderms of the Rockall Trough and adjacent areas

I. Crinoidea, Asteroidea and Ophiuroidea

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Synopsis

Four species of crinoid, forty species of sea star and thirty-six species of brittle star are identified from recent benthic sampling in the deep-sea area to the west of the British Isles, mainly in the Rockall Trough. Of these, one crinoid, nine asteroids and eighteen ophiuroids have not previously been recorded from the seas around the British Isles. The zoogeographical distribution and bathymetric range of each species is summarised as far as was previously known giving the range extension provided by the present records. Notes are also provided on observations on the biology, including the mode of reproduction, of the more abundant species. The records demonstrate a broader bathymetric distribution of juvenile and post larval stages than of the adult populations of some of the more abundant species. A greater diversity of species also is evident from the small number of samples from the western, probably current-swept, side of the Rockall Trough compared with the much larger number of samples collected at similar depths in the east.

Introduction

The cruises of H.M.S. *Lightning* and H.M.S. *Porcupine* in the years 1868–70 in the Rockall Trough and other deep sea areas lying west of the British Isles and of the Iberian peninsula asserted beyond doubt the presence of life at great depths.

Echinoderm data figure prominently in the literature (Lyman, 1882; Sladen, 1889; Thomson, 1872, 1873, 1874) resulting from these cruises that covered deep-sea areas not subsequently sampled by the *Challenger* expedition of 1872–76. Many useful echinoderm records also were made on the cruises of H.M.S. *Knight-Errant* in 1880 and H.M.S. *Triton* in 1882 in the course of exploration of the submarine sill bounding the northern end of the Rockall Trough that was subsequently named the Wyville Thomson Ridge (e.g. Hoyle, 1884; Sladen, 1882). To the authors' knowledge most subsequent records of deep-sea echinoderm fauna from this area have emanated from opportunistic extension into deeper water of essentially coastal sampling programmes. Notable among these are the cruises of the Irish Fisheries Department cruiser *Helga* in the early years of this century. Exploration of some of the outer banks and shelf areas around the northern perimeter of the Rockall Trough has also resulted in many useful records of fauna including echinoderms (Danielssen & Koren, 1884; Süssbach & Breckner, 1911; Pawsey & Davis, 1924). Other records have come from stations worked in the Rockall area in the course of wider ranging cruises, such as those of the *Thor,* and the *Michael Sars* in her Atlantic expedition of 1910, and more recently

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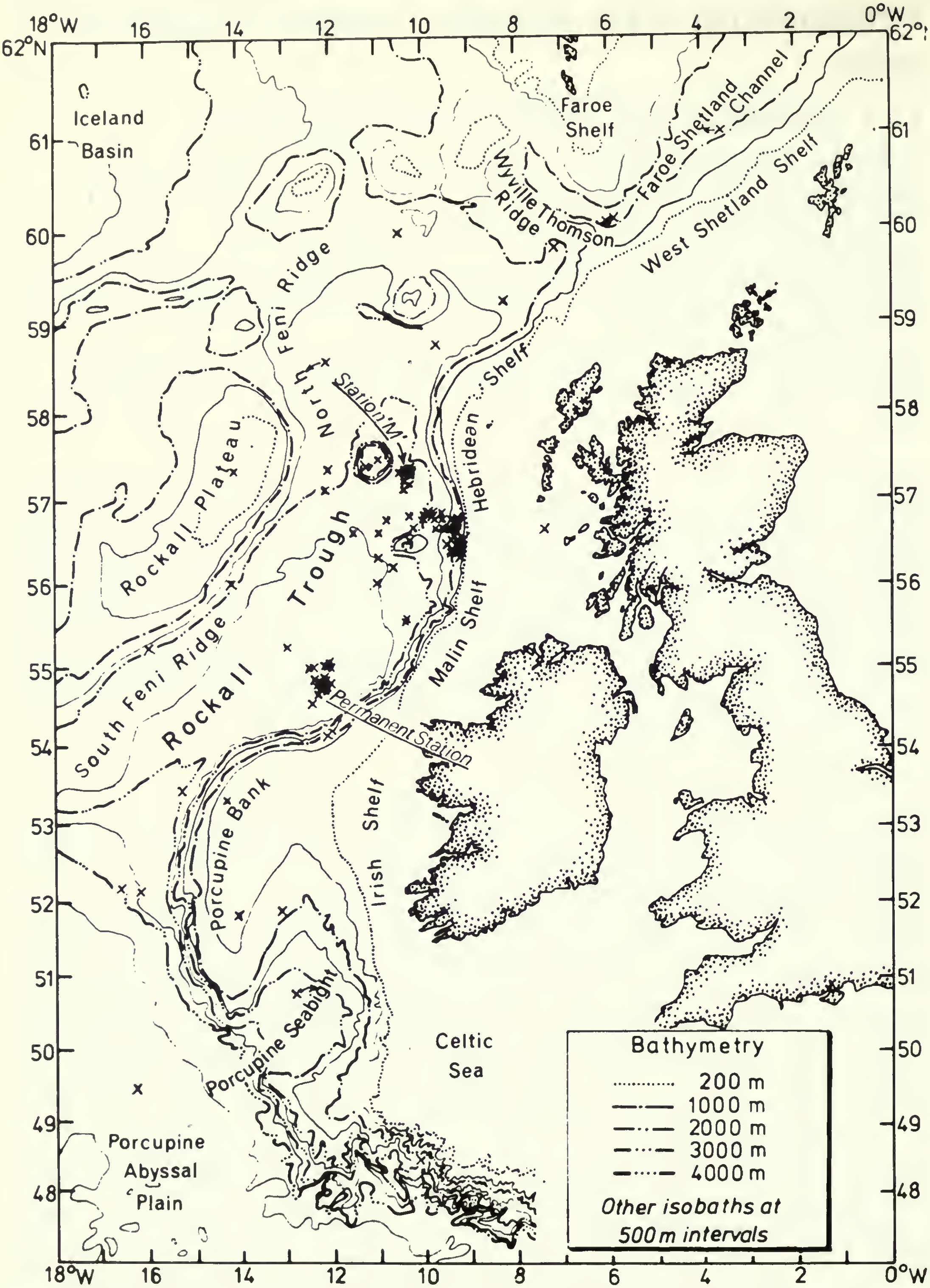
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Iceland Basin
Faroe Shelf
Faroe Shetland Channel
Wyville Thomson Ridge
West Shetland Shelf
Feni Ridge
North
Station 'M'
Hebridean Shelf
Rockall Plateau
Rockall Trough
South Feni Ridge
Malin Shelf
Permanent Station
Porcupine Bank
Irish Shelf
Porcupine Seabight
Celtic Sea
Porcupine Abyssal Plain
Bathymetry
200 m
1000 m
2000 m
3000 m
4000 m
Other isobaths at 500 m intervals

Fig. 1 Bathymetric chart showing Permanent Station and Station 'M' and all other sample stations (crosses).

by the French oceanographic ship *Jean Charcot* in 1969 (Cherbonnier & Sibuet, 1973) and in 1976 (INCAL expedition). Although not extending into the Rockall Trough the sampling in neighbouring northern areas by the major expeditions to the N. Atlantic such as the cruises of the *Voeringen* Norwegian North Atlantic Expedition, 1876–1878, and the Danish *Ingolf* expedition, 1895–6, should also be mentioned in this context.

The Scottish Marine Biological Association (SMBA) in 1973 initiated exploratory biological sampling in the deep waters off the continental shelf as an extension of programmes previously restricted to coastal environments. Subsequent sampling has been undertaken on many cruises mainly on R.R.S. *Challenger,* in the Rockall Trough and the adjacent continental slope off the west of Scotland (Fig. 1). This work has been focussed both as quantitative and seasonal sampling programmes in studies of the structure, reproduction and growth of midwater, demersal and benthic populations of fish and invertebrate species at fixed stations located in the middle and southern part of the Rockall Trough (Gordon, 1979; Gage *et al.,* 1980; Gage & Tyler, 1982; Kawaguchi & Mauchline *a, b* in press). In addition there has been some sampling by the SMBA in the N Feni Ridge and Wyville Thomson Ridge areas, in the Porcupine Seabight and its vicinity, and on the S. Feni Ridge (Fig. 1).

The present account concentrates on echinoderm distributions, because populations of echinoderm species are conspicuous elements of the benthic megafauna, animals easily recognisable in sea-bed photographs). Echinoderms hence may frequently occur in the fish catches obtained by coarse-meshed demersal trawls, such as the large commercial pattern Granton trawl and smaller single-warp otter trawls. Echinoderms also dominate catches made with a 3-metre wide Agassiz trawl. This trawl has been deployed in poor weather that has precluded use of other gear employed in the SMBA programme, such as the epibenthic sled (Hessler & Sanders, 1967) and USNEL 0·25 m^2 Box Corer (Hessler & Jumars, 1974) both of which have the advantage of retaining benthic larval and juvenile stages, many of them identifiable. Results indicate that juvenile stages may extend over a wider area and greater bathymetric range than that of adult specimens caught in trawls. Therefore in describing the distributional range of species it is necessary to distinguish records where larvae or juveniles only have been found from those where adults have been collected, and where presumably a breeding population exists.

In the present account, the geographical distribution and bathymetric data relating to both past and present records are interpreted in relation to the properties and dynamics of water masses, which are relatively well known in the Rockall area (Ellett & Martin, 1973; Roberts, 1975).

Station List

Details of bottom sampling stations worked are listed below. Except for benthic stations 118–125 that were worked from R.R.S. *Shackleton,* all stations listed were worked from R.R.S. *Challenger.* Benthic stations and fishing stations, worked by Dr J. D. M. Gordon of SMBA, are listed separately in chronological order with a prefix to the station number that identifies gear used: ES, epibenthic sled; ABD, anchor-box dredge; SBC, $\frac{1}{4}$ m^2 spade box corer; AT, 3 m Agassiz trawl; GT, Granton trawl; SWT, single warp otter trawl, OTSB, semi-balloon otter trawl 14. For most fish trawls (GT, SWT and OTSB) depths at mid-point of haul is unknown and total depth range of haul is given.

St. No.	Date	Position (at mid-point of track on bottom if applicable)	Depth (m)
Benthic stations			
ES 2	4 June 1973	55°04′N, 12°33′W	2857
ABD 3	5 June 1973	56°46′N, 10°02′W	1997

St. No.	Date	Position (at mid-point of track on bottom if applicable)	Depth (m)
ES 4	5 June 1973	56°52′N, 10°01′W	1993
ES 5	5 June 1973	56°43′N, 09°05′W	763
ES 6	2 July 1973	55°03′N, 12°29′W	*c.* 2900
ES 8	3 July 1973	54°45′N, 12°10′W	*c.* 2900
ES 10	4 July 1973	56°37′N, 10°04′W	*c.* 2540
ES 12	20 Sept. 1973	56°49′N, 10°15′W	2076
ES 14	22 Sept. 1973	56°45′N, 09°46′W	1770
ES 15	22 Sept. 1973	56°44′N, 09°28′W	1632
ES 18	22 Sept. 1973	56°44′N, 09°20′W	1392
ES 20	23 Sept. 1973	56°46′N, 09°17′W	1271
ES 22	23 Sept. 1973	56°41′N, 09°11′W	1028
ES 23	23 Sept. 1973	56°37′N, 09°10′W	704
ABD 24	23 Sept. 1973	56°36′N, 09°13′W	810
ABD 25	23 Sept. 1973	56°36′N, 09°10′W	588
ES 27	3 Nov. 1973	54°40′N, 12°16′W	*c.* 2880
ES 28	3 Nov. 1973	54°33′N, 12°21′W	*c.* 2880
ES 31	20 Mar. 1975	55°03′N, 12°01′W	2875
ES 32	22 Mar. 1975	55°16′N, 12°58′W	2871
ES 33	23 Mar. 1975	56°35′N, 07°16′W	148
ES 34	10 May 1975	56°36′N, 11°30′W	2515
SBC 46	6 Sept. 1975	55°04′N, 12°06′W	2875
SBC 47	6 Sept. 1975	55°03′N, 12°03′W	2875
SBC 48	7 Sept. 1975	55°04′N, 12°04′W	2875
SBC 49	7 Sept. 1975	55°03′N, 12°05′W	2875
SBC 50	7 Sept. 1975	55°04′N, 12°02′W	2875
SBC 51	7 Sept. 1975	55°03′N, 12°03′W	2875
ES 52	15 Nov. 1975	*c.* 54°40′N, 12°16′W	2886
ES 53	15 Nov. 1975	*c.* 54°40′N, 12°16′W	2886
ES 54	17 Nov. 1975	*c.* 54°40′N, 12°16′W	2878
ES 55	17 Nov. 1975	*c.* 54°40′N, 12°16′W	2878
ES 56	1 Mar 1976	*c.* 54°40′N, 12°16′W	2886
ES 57	21 June 1976	*c.* 54°41′N, 12°23′W	*c.* 2900
SBC 58	21 June 1976	54°41′N, 12°17′W	*c.* 2900
ES 59	21 June 1976	54°40′N, 12°20′W	*c.* 2900
SBC 60	23 June 1976	56°35′N, 11°03′W	*c.* 2500
SBC 61	23 June 1976	57°08′N, 12°09′W	*c.* 2000
SBC 62	23 June 1976	57°28′N, 11°00′W	*c.* 610
SBC 63	25 June 1976	56°37′N, 09°49′W	*c.* 1800
SBC 64	26 June 1976	56°38′N, 09°29′W	*c.* 1400
SBC 65	26 June 1976	56°39′N, 09°40′W	*c.* 1600
SBC 66	26 June 1976	56°39′N, 09°23′W	*c.* 1200
SBC67	26 June 1976	56°39′N, 09°13′W	*c.* 1000
SBC 68	1 July 1976	58°42′N, 09°43′W	*c.* 1800
AT 68A	2 July 1976	59°13′N, 08°01′W	1330
ES 69	2 July 1976	59°39′N, 07°12′W	1050
ES 87	4 July 1976	61°13′N, 03°59′W	1050
ES 90	7 July 1976	60°05′N, 05°55′W	1040
AT 90A	7 July 1976	60°05′N, 05°57′W	1040
ES 99	9 July 1976	60°00′N, 10°35′W	1160
ES 105	10 July 1976	58°27′N, 12°35′W	1600
AT 107A	11 July 1976	57°07′N, 12°06′W	*c.* 2000
ES 111	22 Oct. 1976	54°40′N, 12°16′W	2886
ES 112	25 Oct. 1976	55°12′N, 15°50′W	1900

St. No.	Date	Position (at mid-point of track on bottom if applicable)	Depth (m)
ES 113	27 Oct. 1976	57°18′N, 14°07′W	168
AT 114	28 Oct. 1976	56°48′N, 10°54′W	2400
ES 115	28 Oct. 1976	56°29′N, 10°22′W	1000
ES 118	28 Jan. 1977	54°39′N, 12°14′W	2910
AT 119	28 Jan. 1977	54°40′N, 12°14′W	2908
ES 120	28 Jan. 1977	54°39′N, 12°16′W	2911
AT 121	29 Jan. 1977	54°37′N, 12°09′W	2910
ABD 125	30 Jan. 1977	52°56′N, 12°58′W	394
ES 129	7 April 1977	54°39′N, 12°17′W	*c.* 2900
AT 131	7 April 1977	55°03′N, 12°20′W	*c.* 2900
AT 132	8 April 1977	53°14′N, 14°16′W	225
AT 133	8 April 1977	52°30′N, 14°03′W	315
AT134	9 April 1977	54°05′N, 12°06′W	800
ES 135	7 Aug. 1977	54°39′N, 12°16′W	2900
ES 137	22 Feb. 1978	54°34′N, 12°19′W	2900
AT 138	23 Feb. 1978	55°31′N, 10°24′W	2450
AT 139	24 Feb. 1978	55°35′N, 10°25′W	2450
ES 140	13 April 1978	54°40′N, 12°16′W	2912
AT 141	14 April 1978	54°44′N, 12°14′W	2909
ES 143	14 April 1978	54°41′N, 12°14′W	2892
AT 144	19 April 1978	57°13′N, 10°20′W	2240
ES 147	2 June 1978	54°36′N, 12°19′W	2921
SBC 150	3 June 1978	54°37′N, 12°13′W	2916
AT 151	6 June 1978	57°21′N, 10°22′W	2175
ES 152	13 Jan. 1979	54°42′N, 12°02′W	2900
AT 153	15 Jan. 1979	57°20′N, 10°27′W	2200
AT 154	21 May 1979	57°08′N, 10°22′W	2264
SBC 155	4 Aug. 1979	48°27′N, 10°20′W	1330
AT 157	6 Aug. 1979	49°31′N, 13°11′W	1752
AT 161	8 Aug. 1979	50°52′N, 12°22′W	2055
AT 162	9 Aug. 1979	51°50′N, 13°00′W	992
SBC 163	10 Aug. 1979	54°41′N, 12°24′W	2910
ES 164	11 Aug. 1979	54°37′N, 12°22′W	2925
SBC 166	12 Aug. 1979	57°07′N, 10°20′W	2274
AT 167	13 Aug. 1979	57°05′N, 10°25′W	2300
AT 169	28 Feb. 1980	54°40′N, 12°17′W	2910
AT 171	3 Mar 1980	57°16′N, 10°17′W	2225
ES 172	27 May 1980	54°39′N, 12°17′W	2910
AT 175	28 May 1980	57°19′N, 10°16′W	2210
ES 176	28 May 1980	57°15′N, 10°26′W	2245
AT 177	29 May 1980	57°18′N, 10°16′W	2220
ES 178	29 May 1980	56°33′N, 09°17′W	997
ES 180	15 Sept. 1980	54°42′N, 12°11′W	2886
AT 181	16 Sept. 1980	57°19′N, 10°28′W	2220
ES 182	16 Sept. 1980	57°19′N, 10°28′W	2170
ES 184	17 Sept. 1980	57°14′N, 10°24′W	2260
ES 185	10 April 1981	54°44′N, 12°15′W	2907
AT 186	12 April 1981	57°22′N, 10°19′W	2170
ES 190	16 Aug. 1981	54°41′N, 12°18′W	2898
AT 191	17 Aug. 1981	56°00′N, 13°58′W	2190
AT 192	18 Aug. 1981	57°21′N, 12°02′W	1862
AT 194	18 Aug. 1981	57°27′N, 11°10′W	630
AT 195	18 Aug. 1981	57°23′N, 10°27′W	2190

St. No.	Date	Position (at mid-point of track on bottom if applicable)	Depth (m)	
ES 197	19 Aug. 1981	57°21′N, 10°29′W	2220	
AT 198	15 Oct. 1981	57°15′N, 10°20′W	2215	
ES 200	6 Feb. 1982	57°20′N, 10°32′W	2220	
Fishing stations			mean	range
GT 1	19 Mar. 1975	56°37′N, 09°09′W	713	650–805
GT 2	19 Mar. 1975	56°37′N, 09°15′W	1027	972–1084
GT 7	3 Sept. 1975	56°28′N, 09°11′W	689	640–780
GT 8	3 Sept. 1975	56°25′N, 09°20′W	1054	1024–1072
GT 11	7 April 1976	56°32′N, 09°17′W	1014	934–1054
GT 13	8 April 1976	56°33′N, 09°07′W	523	508–543
GT 14	9 April 1976	56°33′N, 09°12′W	761	713–788
GT 15	24 June 1976	56°28′N, 09°11′W	720	672–740
GT 16	25 June 1976	56°25′N, 09°20′W	958	916–992
GT 17	25 June 1976	56°28′N, 09°27′W	1237	1190–1296
SWT 10	5 Aug. 1977	56°51′N, 09°58′W	2018	2000–2030
SWT 11	6 Aug. 1977	56°03′N, 11°05′W	2530	2500–2560
SWT 12	9 Aug. 1977	53°25′N, 15°24′W	2996	2980–3000
SWT 13	9 Aug. 1977	52°04′N, 16°09′W	3463	3425–3500
SWT 15	11 Aug. 1977	49°30′N, 16°12′W	4810	constant
AT 1	19 Oct. 1977	56°24′N, 09°12′W	750	—
AT 3	20 Oct. 1977	56°23′N, 09°18′W	1000	—
SWT 16	21 Oct. 1977	56°12′N, 10°57′W	2441	2400–2490
SWT 17	22 Oct. 1977	56°49′N, 09°55′W	1977	1940–2020
SWT 18	22 Oct. 1977	56°46′N, 09°42′W	1809	1785–1845
SWT 27	4 May 1978	54°26′N, 12°52′W	2965	constant
SWT 32	31 Oct. 1978	56°48′N, 09°56′W	2006	1995–2020
OTSB 51001	30 April 1981	54°45′N, 12°24′W (starting position)	2890	2885–2895

List of Species

- Class Crinoidea
  - Order Millericrinida
    - Family Bathycrinidae
      - *Rhizocrinus lofotensis* M. Sars
  - Order Comatulida
    - Family Pentametrocrinidae
      - *Thaumatocrinus jungerseni* A. H. Clark
    - Family Antedonidae
      - *Heliometra glacialis* (Owen)
      - *Hathrometra sarsi* (Düben & Koren)
- Class Asteroidea
  - Order Paxillosida
    - Family Luidiidae
      - *Luidia sarsi* (Düben & Koren)
      - *Luidia ciliaris* (Philippi)
    - Family Astropectinidae
      - *Astropecten irregularis* (Pennant)
      - *Bathybiaster vexillifer* (Wyville Thomson)
      - *Plutonaster bifrons* (Wyville Thomson)
      - *Dytaster insignis* (Perrier)
      - *Psilaster andromeda* (Müller & Troschel)
      - *Psilaster patagiatus* Sladen
    - Family Porcellanasteridae
      - *Porcellanaster ceruleus* Wyville Thomson
      - *Hyphalaster inermis* Sladen
  - Order Notomyotida
    - Family Benthopectinidae
      - *Benthopecten simplex* (Perrier)
      - *Pectinaster filholi* Perrier
      - *Pontaster tenuispinus* (Düben & Koren)
  - Order Valvatida
    - Family Odontasteridae

Hoplaster spinosus Perrier
Odontaster sp.
Family Radiasteridae
?*Radiaster tizardi* (Sladen)
Family Goniasteridae
Pseudarchaster parelii (Düben & Koren)
Pseudarchaster gracilis (Sladen)
Paragonaster subtilis (Perrier)
Plinthaster dentatus (Perrier)
Evoplosoma scorpio Downey
Family Poraniidae
Porania pulvillus O. F. Müller
Order Spinulosida
Family Pterasteridae
Pteraster militaris (O. F. Müller)
Pteraster pulvillus M. Sars
Pteraster reductus Koehler
Pteraster sp. aff. *P. acicula* (Downey)
Hymenaster membranaceus Wyville Thomson
Hymenaster pellucidus Wyville Thomson
Hymenaster gennaeus H. L. Clark
Hymenaster rex Perrier
Family Solasteridae
Crossaster squamatus (Döderlein)
Family Echinasteridae
Henricia sanguinolenta (O. F. Müller)
Henricia abyssicola (Norman)
Order Forcipulatida
Family Brisingidae
Brisinga endecacnemos Asbjörnsen
Brisingella coronata G. O. Sars
Freyella spinosa Perrier
Freyella sexradiata (Perrier)
Family Asteriidae
Hydrasterias sexradiata (Perrier)
Stichastrella rosea (O. F. Müller)
Family Zoroasteridae
Zoroaster fulgens Wyville Thomson

Class Ophiuroidea
Suborder Euryalida
Family Asteronychidae
Asteronyx loveni Müller & Troschel
Astrodia tenuispina Verrill
Family Asteroschematidae
Asteroschema inornatum Koehler
Family Gorgonocephalidae
Gorgonocephalus caputmedusae (Linnaeus)
Order Ophiurida
Family Ophiacanthidae
Ophiotrema alberti Koehler
Ophiomyces grandis Lyman
Ophiacantha abyssicola G. O. Sars
Ophiacantha bidentata (Retzius)
Ophiacantha crassidens Verrill
Ophiacantha cuspidata Lyman
Ophiacantha simulans Koehler
Ophiacantha aculeata Verrill
Ophiolimna bairdi (Lyman)
Family Ophiactidae
Ophiactis abyssicola (M. Sars)
Ophiactis balli (Thompson)
Family Amphiuridae
Amphiura otteri Ljungman
Amphiura fragilis Verrill
Amphiura griegi Mortensen
Amphipholis squamata (Delle Chiaje)
Subfamily Amphilepidinae
Amphilepis ingolfiana (Mortensen)
Family Ophiochitonidae
Ophiochiton ternispinus Lyman
Family Ophiuridae
Subfamily Ophiurinae
Ophiopleura inermis (Lyman)
Ophiopleura borealis Danielssen & Koren
Homalophiura tesselata (Verrill)
Amphiophiura convexa (Lyman)
Amphiophiura saurura (Verrill)
Stegophiura macrarthra H. L. Clark
Ophiocten gracilis G. O. Sars
Ophiocten hastatum Lyman
Ophiura affinis Lütken
Ophiura carnea Lütken
Ophiura irrorata (Lyman)
Ophiura imprudens (Koehler)
Ophiura ljungmani (Lyman)
Ophiura ophiura (Linnaeus)
Subfamily Ophiolepidinae
Ophiomusium lymani Wyville Thomson

Systematic Account

The following account aims to summarise known distributional records for the individual species together with observations related to the biology of the more abundant ones, including the colour of fresh material if this information is not given by Mortensen (1927).

Throughout, taxonomic references are kept to a minimum by citing, where available, one or more works containing a good description from which the original description and synonymy may be traced. After these citations the sampling stations from which each species has been collected are listed together with the total number of specimens, adults and juveniles, in parentheses. Records from benthic stations are followed by those for fishing stations, which include two Agassiz trawl hauls. Where juveniles only were collected, this is indicated but the term juvenile is used only as a guide and is based arbitrarily on size. The number of specimens has no quantitative significance in comparisons between samples because for most epibenthic sledge hauls a partial sorting only of the catch has been achieved. Total depth range of the present records is given in square brackets after this listing. Details of hauls, including depth range and positional coordinates are listed on pp. 265–268.

Systematic structure of the class Crinoidea follows A. M. Clark (1970*b*); that of the Asteroidea, Downey (1973), Clark (1981) and Blake (1981); while for the Ophiuroidea, including family and subfamily names, we follow Fell (1960). References to the size of animals refer to disk diameter of brittle stars and arm radius, R (measured from arm tip to the centre of the disk) and the interradius, r, of sea stars.

Although all co-authors of the present study have been involved in the preparation and revision of the text, taxonomic responsibility for the identifications of the crinoids and most of the asteroids is taken by A.M.C. and for the ophiuroids by G.L.J.P.

Examples of all species referred to in the present account have been or will be deposited with the British Museum (Natural History).

Class **CRINOIDEA**

Order **MILLERICRINIDA**

Family **BATHYCRINIDAE**

Rhizocrinus lofotensis M. Sars, 1868

See: A. M. Clark, 1970*b* : 19–22, fig. 4, map 2.

Samples. ES 18 (3), ES 20 (8). [1271–1392 m]

Distribution. Recorded from the W coast of Norway, the Rockall Trough area, Iceland, Greenland and the eastern side of North America. Depth range off Norway includes the minimum, 140–700 m, while those from both sides of Greenland include the maximum of 3135 m (*Ingolf* st. 37) but other records east of Iceland rarely much exceed 1200 m. [Carpenter's record from NE Brazil mentioned by A. M. Clark (1970*b*) was referred to *Democrinus* by A.M.C. (1977)].

Previous records from the Rockall Trough area include *Lightning* and *Knight Errant* material from 61°02´N, 12°04´W, 1990 m and *c*.60°N, 07°W, *c*.960 m (Carpenter, 1884) and *Thor* st. 99, 61°15´N, 09°35´W, 872 m, recorded by A. H. Clark (1923) who earlier (1913) recorded one specimen from *Helga* st. CXX, 53°58´N, 12°24´W, 687 m. The latter record probably validates Kemp's (1905) provisional record from '64 miles NW by N of Cleggan Head' (*c*.54½°N, 11½°W), 364 m.

The present sample from the Hebridean slope (56°46´N), consists only of calyces and separate stalk fragments.

Remarks. We retain the familiar and historic generic name *Rhizocrinus* M. Sars, 1868, although according to Roux (1976) it should probably be treated as a junior synonym of *Conocrinus* d'Orbigny, 1850, because of the fused calyx plates in both nominal genera. However, in 1978 Roux listed *Rhizocrinus* with *R. lofotensis* among the Bathycrinidae. *Conocrinus* was known only from lower Caenozoic fossil species until Roux ascribed to it two recent species from the Bay of Biscay which he named *C. cherbonnieri* and *C. cabiochi*. The former is based on a single incomplete specimen from the French research ship *Thalassa* st. Z397, 47°33·8´N, 07°12·6´W, 511 m; superficially very similar to *R. lofotensis* but said to differ in the joint structure of the columnals.

Order **COMATULIDA**

Family **PENTAMETROCRINIDAE**

Thaumatocrinus jungerseni A. H. Clark, 1923

See: A. H. Clark, 1923 : 13–17, figs 2–4; A. M. CLark, 1980 : 204–205.

Samples. SWT 12 (8), SWT 13 (2). [2980–3000 m; 3425–3500 m]

Distribution. Previously known from the Denmark Strait, NW and SW of Iceland and far to the west of Ireland (*c.*53°N, 20°W) in 823–2734 m.

The present new records from the Porcupine Seabight from between 2980 m and 3500 m depth extend the geographical range eastwards and the lower limit of the bathymetric range. However, an unpublished record exists of four specimens from R.R.S. *Discovery* station 9640/1, (50°05′ N, 13°51′ W, 3749–3757 m depth, soft mud) that were identified by A.M.C.

Family **ANTEDONIDAE**

Heliometra glacialis (Owen, 1833)

See: A. M. Clark, 1970*b* : 24–27, fig. 5, map 3.

Sample. ES 112 (1). [1900 m]

Distribution. Previously known primarily from the Arctic where it is circumpolar, extending south in the NW Atlantic to George's Bank off Cape Cod, but in the east only to the Faroe Channel and northernmost Norway; 14–1358 m; usually on gravel with sand and mud or loose stones.

The present record from the South Feni Ridge extends both the known range southwards to latitude 55°N in the NE Atlantic and the lower limit of the bathymetric range.

Remarks. An arcturid amphipod, identified as such by Dr R. J. Lincoln of the British Museum (Natural History), was found associated with this specimen.

?***Hathrometra sarsi*** (Düben & Koren, 1846)

See: A. M. Clark, 1970*b*: 42–45, figs 15, 16 for *Poliometra prolixa*, 39–42, fig. 14 for *Hathrometra sarsi,* 36–39, fig. 12 for *Leptometra celtica.*

Sample. ES 20 (1). [1271 m]

Remarks. The single badly broken specimen has lost all the cirri completely and the arms from the first or second syzygy (brachials 3 or 9). An arm fragment from the same sample has pinnules with very long pinnulars. This fact and the blunt conical form of the centrodorsal suggest identity with *Poliometra prolixa* (Sladen) or *Hathrometra sarsi* (Düben & Koren), possibly *Leptometra celtica* (Barrett & McAndrew) but the depth and latitude are both too high to make this last identity likely. A. H. Clark (1913) recorded *P. prolixa* from *Silver Belle* st. 9, 60°18′N, 04°43′W, 905 m and referred to '*Hathrometra* sp.' single specimens from *Helga* sts SR 353 and 506 at *c.*50½°N, 11°W, down to 990 and 1230 m. In 1967 (*in* Clark & Clark) he cited both of these as *H. sarsi* without question, prompting A.M.C. (1970*b*) to repeat this southern record, though clearly it needs confirmatory material. Otherwise, the southernmost record of *H. sarsi* to the west of the British Isles is from *Triton* st. 2, 59°37′30′′ N, 06°19′ W, 969 m very close to *Porcupine* st. 54, 633 m where *P. prolixa* was taken (Clark & Clark, 1967). Of the two species, *H. sarsi* is much more likely to extend further south since it extends in Scandinavia to Danish waters whereas *P. prolixa* is limited to northernmost Norway. Morphologically, the two are distinguished by the more regular arrangement of the cirri in *Poliometra,* tending to form vertical lines on the centrodorsal, especially in larger specimens; on this count, the present specimen inclines towards *Hathrometra.*

Class **ASTEROIDEA**

Order **PAXILLOSIDA**

Family **LUIDIIDAE**

Luidia sarsi Düben & Koren, 1845

See: Süssbach & Breckner, 1911 : 210–214; A. M. Clark, 1982 : 175–80, figs 1c, 2c, g, 3m–o, v, 6.

SAMPLES. ES 33 (4), ES 113 (juvenile, 1). [148 m, 168 m]

DISTRIBUTION. From the Faroe Bank Channel eastwards to Trondheim, Norway and southwards to the Mediterranean, Cap Blanc and the Azores; 9–1300 m; usually on muddy rather than clean sand, or on clay. *Luidia sarsi* was taken by the *Helga* at many stations worked off the west coast of Ireland.

The present records from the Hebridean Sea and the Rockall Bank are well within the known bathymetric range and its present occurrence further north and west is to be expected (Mortensen, 1927).

Luidia ciliaris (Philippi, 1837)

See: Süssbach & Breckner, 1911 : 209–210; Mortensen, 1927 : 70, fig. 39a.

SAMPLE. GT 1 (1). [650–805 m]

DISTRIBUTION. From the Faroe Channel east to southern Norway and south to the Mediterranean, Canary Is. and Azores; previously recorded from 1 to 400 m (Mortensen, 1927).

The present record surprisingly extends the deeper limit to at least 650 and possibly 805 m depth; substratum usually fine gravel, often with little or no mud.

Family **ASTROPECTINIDAE**

Astropecten irregularis (Pennant, 1777)

See: Süssbach & Breckner, 1911 : 203–207; Mortensen, 1927 : 57–58, fig. 32.

SAMPLES. AT 133 (7 var. *pentacanthus*). GT 1 (1), GT 7 (3 var. *pentacanthus*). [315 m to 650–805 m]

DISTRIBUTION. Coastal distribution from Norway south to Morocco; 10–1000 m. It is said to prefer a sandy bottom (Mortensen, 1927).

The presence of this well-known species on the upper Hebridean slope down to between 650 and 805 m depth is not unexpected. The specimens from GT 7 and AT 133 lack the large spine on the superomarginals and therefore agree with the variety *pentacanthus* (Delle Chiaje).

Bathybiaster vexillifer (Wyville Thomson, 1873)

See: Grieg, 1921 [1932]: 16–18; Mortensen, 1927 : 61–63, figs 34, 35 (as *B. robustus* and *B. vexillifer*).

SAMPLES. ES 10 (1), ES 34 (3), AT 90A (1), AT 107A (2), AT 114 (6), AT 138 (juvenile, 1), AT 139 (6), AT 144 (23), AT 151 (15), AT 153 (22), AT 154 (34), AT 161 (6), AT 162 (8), AT 167 (9), AT 171 (28), AT 175 (10), ES 176 (4), AT 177 (11), ES 178 (2), AT 181 (25), ES 182 (1), ES 184 (7), AT 186 (10), AT 191 (juvenile, 1), AT 192 (6), AT 195 (17), ES 197 (20), AT 198 (9), ES 200 (3). SWT 10 (1), SWT 11 (1), SWT 16 (28), SWT 17 (3). [992 m–2540 (?2560) m]

DISTRIBUTION. This purely circumpolar Arctic/N boreal species is known to extend south to North Carolina in the west and the Bay of Biscay in the east Atlantic; 630–3100 m (shallower depths only within the Arctic); on soft muddy sediments.

Our shallowest record at 992 m on the Porcupine Bank does not accord with a distribution limited by a temperature of 1–4°C suggested by Cherbonnier & Sibuet (1973) since temperatures in the Rockall Trough between 900 and 1000 m, although showing little seasonal variation, may exceed 8°C (Ellett & Martin, 1973).

Reproduction. Histological examination of the gonads of individuals collected in a time series from St. 'M' show no evidence of reproductive synchrony within or between samples taken at different times of the year; the sexes are separate and the large size of ripe oocytes (*c.* 1000 μm diameter) suggests direct, external lecithotrophic development (Tyler, Pain & Gage, 1982*a*). There is no evidence of brooding of young.

Plutonaster bifrons (Wyville Thomson, 1873)

See: Grieg, 1921 [1932]: 13–14; Mortensen, 1927 : 63–64.

Samples. ES 4 (4), ES 6 (juvenile 1), ES 18 (1), ES 20 (3), AT 68A (1), ES 69 (1), ES 105 (1), AT

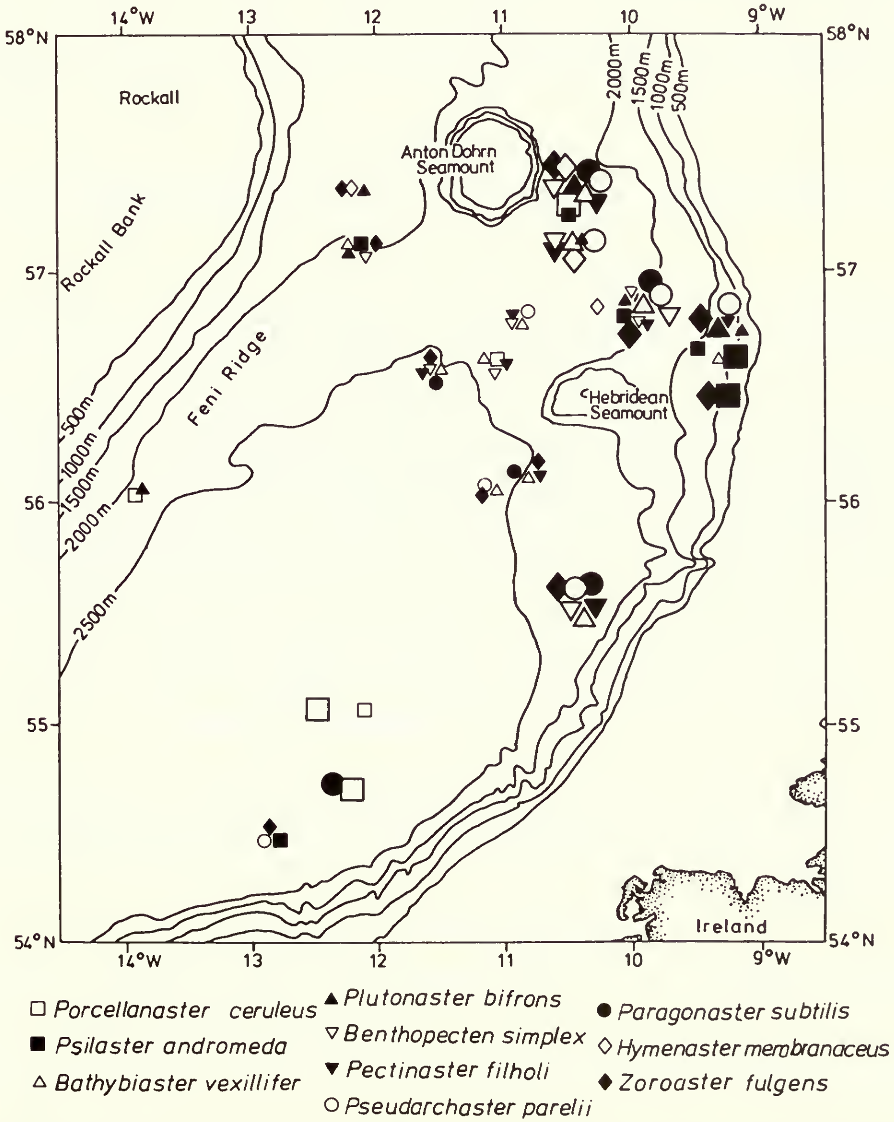
14°W
13
12
11
10
9°W
58°N
57
56
55
54°N
Rockall
Rockall Bank
Feni Ridge
Anton Dohrn Seamount
Hebridean Seamount
Ireland
2000m
1500m
1000m
500m
2500m
□ Porcellanaster ceruleus
■ Psilaster andromeda
△ Bathybiaster vexillifer
▲ Plutonaster bifrons
▽ Benthopecten simplex
▼ Pectinaster filholi
○ Pseudarchaster parelii
● Paragonaster subtilis
◇ Hymenaster membranaceus
◆ Zoroaster fulgens

Fig. 2 Chart of central part of Rockall Trough showing station locations for records of the ten most abundant sea star species. Larger symbols denote records from more than one sample taken on or near the position.

107A (6), AT 144 (10), AT 151 (7), AT 153 (20), AT 154 (5), AT 161 (10), AT 167 (15), AT 171 (17), AT 175 (5), ES 176 (2), AT 177 (12), AT 181 (15), ES 182 (1), ES 184 (2), AT 186 (24), AT 191 (4), AT 192 (69), AT 195 (17), ES 197 (2), AT 198 (3), ES 200 (1). GT 17 (4), SWT 10 (40), SWT 11 (12), SWT 17 (3), SWT 18 (38), SWT 27 (4), SWT 32 (12), AT 3 (5). [1000–2965 m]

DISTRIBUTION. Previously known from the Faroe Channel to South Africa; 800–2500 m; on soft muddy sediments.

Our records for this species extend the lower limit of the known range to 2965 m. The bathymetric range of these records covers a temperature range of around 3·5–7°C in the Rockall Trough (Ellett & Martin, 1973). Farran (1913) indicates from trawlings in the Porcupine Seabight that *P. bifrons* does not usually occur off the Irish coast at depths less than 500 fathoms (914 m).

REPRODUCTION. The sexes are separate, and preliminary examination of the serially arranged gonads lying on the underside of the dorsal arm surface of females shows numerous small oocytes with a maximum size of about 120 μm diameter. There is also evidence of reproductive seasonality, with spawning in spring (Tyler, Pain & Gage, 1982*b*; Tyler & Pain, 1982*a*). Sibuet & Cherbonnier (1972) describe, with SEM figures, the post-metamorphosal stages.

REMARKS. Specimens of *P. bifrons* from St. 'M' contain a small flatworm in the body cavity; this appears not to affect gonadal development nor to harm the host in any way.

Dytaster insignis (Perrier, 1884)

See: Perrier, 1884 : 253, pl. 9, fig. 5; Downey, 1973 : 35–36, pl. 9, figs C, D.

SAMPLES. ES 53 (1), ES 55 (2), ES 56 (1), ES 120 (2), AT 121 (15), ES 129 (1), AT 131 (2), AT 153 (1), AT 181 (1), ES 182 (1). SWT 13 (3), SWT 27 (1). [2170 m to 3425–3500 m]

DISTRIBUTION. Downey (1973) has synonymised several previously described nominal N Atlantic species of this exclusively deep-water genus, including *D. biserialis* Sladen, the oldest name being *D. insignis.* This has a wide distribution throughout the N Atlantic deep sea and possibly extends over the entire Atlantic; on soft deep-sea ooze. *Dytaster biserialis* was recorded from the NE Atlantic from depths of 3645 m and 4360 m (Mortensen, 1927).

The present records confirm that this species has an essentially abyssal distribution.

REPRODUCTION. Histological study of the gonads of *D. insignis,* which are serially arranged along the underside of the dorsal surface of the arm, suggests a high fecundity, probably in excess of 10^6 eggs/individual. Maximum egg size is 120 μm, suggesting indirect, possibly pelagic, development (Tyler, Pain & Gage, 1982*b*; Tyler & Pain, 1982*a*). The latter authors also indicate that this species shows some form of gametogenic synchrony in the population sampled.

REMARKS. Species of the genus *Dytaster* are thought to be omnivorous scavengers; fragments of algae, foraminiferous worm tubes and molluscs having been found in the stomach (Downey, 1973) while Bruun & Wolff (1961) give a photograph with a specimen ingesting a large fish bone.

Psilaster andromeda (Müller & Troschel, 1842)

See: Süssbach & Breckner, 1911 : 208–209; Grieg, 1921 [1932]: 18–19 (?St. 70); Mortensen, 1927: 59–60, fig. 33; D'yakonov, 1950 : 31.

SAMPLES. ES 23 (3), AT 68A (1), AT 107A (5), AT 186 (3), AT 192 (29; ? [juveniles] 5). GT 2 (1), GT 7 (1), GT 11 (5), GT 14 (2), GT 15 (1), GT 16 (4), SWT 18 (7), SWT 27 (4), AT 1 (3). [640–780 m to 2965 m]

DISTRIBUTION. Previously known from the southern Barents Sea south to Senegal and from the Azores; 20–1853 m. If *P. florae* Verrill, 1878 proves to be a synonym, then also from the western N Atlantic. On ooze and other soft muddy sediments.

The present records extend the lower limit of the known range of *P. andromeda* to 2965 m depth. Our shallowest record, between 640 and 780 m, roughly accords with that of specimens collected by the *Helga* off the west coast of Ireland (Farran, 1913). In more northerly latitudes it may extend into considerably shallower depths.

Reproduction. The sexes are separate. Mortensen (1927) suggested that the large yolky eggs of this species indicate a direct development without a larval stage. Tyler, Pain & Gage (1982*b*) and Tyler & Pain (1982*a*) have noted a maximum egg size of 950 µm in histological preparations of the gonad of females. Hence, direct development with a benthic stage seems likely.

Remarks. Our specimens were as described by Mortensen (1927), being slimy-skinned and pale pink or dirty white in colour, although D'yakonov (1950) describes Russian specimens as a bright red in life.

Psilaster andromeda is known as the host of an unidentified species of the parasitic barnacle genus *Dendrogaster* which causes severe regression of the gonads (P.A.T. personal observation).

Psilaster patagiatus Sladen, 1889

See: Grieg, 1921 [1932]: 19 (as *Psilasteropsis patagiatus*); Mortensen, 1927: 65–66, fig. 37 (as *Persephonaster patagiatus*); Downey, 1973: 32, pl. 8, figs A, B.

Samples. ES 15 (2), ES 18 (3), AT 192 (1). SWT 18 (1). [1392–1862 m]

Distribution. From the Rockall Trough, Porcupine Seabight (Farran, 1913) to the Azores and Cape Verde Islands (Koehler, 1909); and in the Gulf of Mexico and Caribbean Sea off Venezuela where the depths recorded are only 730 m and 915 m; on soft muddy sediments. Mortensen (1927) gives the lower bathymetric limit as 2165 m.

There is, however, a complication about the limits of this species. Although Downey (1973) has referred West Indian specimens to *P. patagiatus,* H. L. Clark (1941) used another name *spinulosus*, which he referred to *Persephonaster* together with *patagiatus*, for Cuban specimens from *c.*1000 m. He also thought the Azores specimens belonged to a third species. A.M.C. (MS) has provisionally named as *P. patagiatus* a *Discovery* specimen from the Canaries. Downey (1973) queried the Cape Verde area as type locality for *P. patagiatus* but this identification, if correct, would support it.

Family **PORCELLANASTERIDAE**

Porcellanaster ceruleus Wyville Thomson, 1877

See: Lieberkind, 1935: 5–19, pl. 2 figs 1–8, pl. 3 fig. 12, pl. 5 figs 16–17; Madsen, 1961: 1123–142, figs 22–24.

Samples. ES 2 (18), ES 4 (5), ES 6 (835), ES 8 (22), ES 10 (101), ES 27 (41), ES 34 (4), SBC 49 (1), ES 52 (7), ES 55 (28), ES 56 (50), SBC 58 (1), ES 59 (20), ES 111 (26), ES 118 (11), AT 121 (6), ES 129 (39), ES 135 (29), ES 137 (53), ES 140 (150), AT 141 (2), ES 143 (12), ES 147 (46), ES 152 (61), ES 164 (91), ES 169 (68), ES 172 (71), ES 176 (2), ES 180 (110), ES 184 (3), ES 185 (195), ES 190 (63), AT 191 (3), ES 197 (2). SWT 13 (1). [1993 m to 3425–3500 m]

Distribution. A cosmopolitan deep-sea species, except in Antarctic waters; known from 1160–6040 m depth; on soft deep-sea ooze.

Individuals of this small species (max. R *c.* 36 mm, Madsen, 1961) were most numerous in epibenthic sled hauls from the Permanent Station, decreasing in number in sled hauls from shallower stations.

Remarks. The specific name of *ceruleus,* unnecessarily amended to *'caeruleus'* by Sladen (1889), was derived from the sky blue colouring of the sediment filling the stomach of the type specimen from *Challenger* st. 45, off Delaware, NW Atlantic. The stomachs of this deposit-feeding species in the recent samples were likewise filled with mud, but of the khaki brown colour of the *Globigerina* ooze characteristic of the deep-sea sediment in the Rockall Trough.

Hyphalaster inermis Sladen, 1883

See: Madsen, 1961: 58–72, figs 6, 7, pls 1–3, 13, figs 3, 4.

SAMPLES. ES 147 (? [juvenile] 1). SWT 13 (1). [2921 m to 3425–3500 m]

DISTRIBUTION. Previously known from the West European Basin north to *c.* 47°N, 08°W, south to the Guinea Basin, also from the Labrador Basin and mid N Atlantic (*c.* 54°N, 27–28°W) and from the Indo-Pacific; 2280–5430 m; on mud, *Globigerina* ooze or calcareous clay.

The present records extend the known range slightly in the NE Atlantic.

REPRODUCTION. Egg size reaches 0·5–0·6 mm with presumably direct development (Madsen, 1961).

REMARKS. The specimen from SWT 13 has R 39 mm, r 19 mm. The specific identity of the single juvenile from ES 147 remains uncertain.

Order **NOTOMYOTIDA**

Family **BENTHOPECTINIDAE**

Benthopecten simplex (Perrier, 1881)

See: Mortensen, 1927 : 74–75, fig. 41 (as *B. armatus* (Sladen)); A. M. Clark, 1981 : 130–134.

SAMPLES. ES 4 (13), ES 10 (juvenile 1), ES 34 (2), AT 107A (3), AT 114 (5), AT 138 (5), AT 139 (10), AT 144 (117), AT 151 (25), AT 153 (71), AT 154 (49), AT 161 (47), AT 167 (33), AT 171 (110), AT 175 (62), ES 176 (56), AT 177 (171), AT 181 (98), ES 182 (7), ES 184 (16), AT 186 (139), AT 191 (juveniles, 45), AT 192 (93), AT 195 (113), ES 197 (27), AT 198 (20; ? [juveniles], 10), ES 200 (11). SWT 13 (2), SWT 16 (1), SWT 17 (1), SWT 18 (19), SWT 32 (10). [1785–1845 m to 3325–3500 m]

DISTRIBUTION. East of Cape Cod south to the Gulf of Mexico, Colombia and Guyana Basins, and south of Iceland (*c.* 62°N, 19°30′W) and the Rockall Trough south to the Gulf of Guinea; 1175 m to 2735–3670 m, this lower limit being derived from *Pillsbury* st. 681, off Surinam.

Our deepest record is from a trawling taken at the deep water confluence of the Rockall Trough with the Porcupine Abyssal Plain. The most northerly record was from the Feni Ridge at *c.* latitude 57°20′N in *c.* 1860 m depth close to *Michael Sars* st. 101 where Grieg (1921) also reported collecting 12 specimens of *Benthopecten.* Both the present and previous records strongly suggest a distribution centred on depths of *c.* 2000 m at temperatures below about 4°C in the N Atlantic, on soft muddy sediments.

Benthopecten simplex is fairly abundant in Agassiz hauls from st. 'M' and these samples usually include substantial, though varying, numbers of juveniles with a range of sizes (Pain, Tyler & Gage, 1982*b*).

Maximum size (R) recorded is *c.* 130 mm (Tyler, Pain & Gage, 1982*b*) whereas that of the few *Sarsia* specimens from the Bay of Biscay (E. C. Southward, personal communication) is only 30–35 mm. Sladen's *Challenger* expedition specimens, of *armatus,* are also smaller than equatorial Atlantic ones where R max. = *c.* 150 mm (A. M. Clark, 1981).

REPRODUCTION. The sexes are separate and no seasonal periodicity is evident from the histological comparison of the gonads of specimens taken at different times of the year; maximum oocyte size is 950 μm, suggesting non-pelagic, possibly lecithotrophic, direct larval development (Tyler, Pain & Gage, 1982*b* as *B. armatus*; Pain, Tyler & Gage, 1982*b*).

REMARKS. Farran (1913) and Mortensen (1927) used the name *B. armatus* (Sladen, 1889) while Grieg (1921) used *B. spinosus* Verrill (1884). A. M. Clark (1981) believes all NE Atlantic and some NW Atlantic specimens of *Benthopecten* to be conspecific with the tropical Atlantic *B. simplex* (Perrier, 1881) of which *armatus* is a synonym but *B. spinosus,* only known from the NW Atlantic, is a distinct species.

Pectinaster filholi Perrier, 1885

See: Sladen, 1889: 43–47, pl, 8, figs 3, 4, pl. 12, figs 3, 4 (as *Pontaster forcipatus*); A. M. Clark, 1981 : 119–121.

SAMPLES. ES 10 (6), ES 34 (7), AT 114 (13), AT 138 (3), AT 139 (14), AT 141 (juvenile 1), AT 144 (14), AT 153 (5), AT 154 (11), AT 157 (1), AT 161 (7), AT 167 (3), AT 171 (3), AT 175 (3), ES 176 (1; ? [juvenile] 13), AT 177 (4), AT 181 (5), ES 182 (1), ES 184 (4; ? [juveniles] 14), ES 185 (juveniles, 2), AT 186 (1), AT 198 (8). SWT 16 (38), SWT 17 (7). [1752–2909 m]

DISTRIBUTION. Previously recorded (A. M. Clark, 1981) from all four quadrants of the Atlantic, north to *c.* 60°N, 20°W (S from Ireland); 1260 m–4850 m, the maximum being the isolated record for the holotype of *Pontaster pristinus* Sladen, off the River Plate, the deepest other record being 3430 m. Cherbonnier & Sibuet (1973) cite a minimum depth of 1152 m but details of this record have not been traced; on mud or *Globigerina* ooze.

This species was present in Agassiz trawls from St. 'M'. Elsewhere, adult specimens were taken from a number of locations in the Rockall Trough and Porcupine Seabight area between 1752 m and 2540 m. Juveniles were also taken between 2200 m and 2900 m.

Cherbonnier & Sibuet (1973) recorded *P. filholi* sensu stricto from NW Africa, the Azores and the southern Bay of Biscay, their record on map 4 of the results of the Noratlante Expedition being misplaced to west of Brittany, if the station list data are correct. A. M. Clark (1981) returned *Pontaster forcipatus* Sladen, 1889, as well as *P. pristinus*, to the synonymy of *Pectinaster filholi,* bringing in records from eastern North America and South Africa, as well as two *Discovery* records from the central North Atlantic to the far west of Ireland and south from Iceland. Although no *Helga* specimens were recorded by Farran (1913), a small one was found in the British Museum collections from the sample of *Benthopecten armatus* [*simplex*] from st. SR 944, SW of Ireland.

REPRODUCTION. The sexes are separate; preliminary studies on the gametogenic cycle (Pain, Tyler & Gage, 1982*b*) indicate a maximum oocyte size of 850 µm, suggesting a non-pelagic, possibly lecithotrophic or direct development. Brooding has not been recorded. Individuals become mature at *c.* r 3 mm. Size frequencies in the sample time series from St. 'M' indicate a low, probably year-round recruitment by young of around r 1 mm. Adult size structure is variable in the samples which suggests a possibly patchy demographic composition on the bottom (Pain, Tyler & Gage, 1982*b*).

Pontaster tenuispinus (Düben & Koren, 1846)

See: Sladen, 1889 : 28–29, 29–30, pl. 6, fig. 7, pl. 7, figs 3, 4 (var. *platynota*), 35–38, pl. 6, figs 3, 4, pl. 7, figs 1, 2 (as *P. limbatus*); Süssbach & Breckner, 1911 : 201–202; Mortensen, 1927 : 72–73, fig. 40.

SAMPLES. ES 23 (4), ABD 25 (1), ES 87 (5 var. *platynota*), AT 90A (? [juveniles var. *platynota*] 3), AT 107A (1). GT 1 (4), GT 7 (4), GT 13 (1), GT 14 (2), GT 15 (4), AT 1 (74), AT 3 (2). [508–543 m to 2000 m]

DISTRIBUTION. Circum-arctic extending south in the Atlantic to the latitude of Cape Cod in the west and the eastern slope of the Bay of Biscay (*c.* 44°N) in the east, 16–*c.* 2000 m, (2330 m according to Perrier, 1894), rarely <200 m, except in arctic waters. The records of Farran (1913) are from *c.* 400–800 m in the Porcupine Seabight. The Porcupine record (Sladen, 1889) from 100–150 fathoms, 183–274 m, off Valentia, SW Ireland is surprisingly shallow. The round numbers, in fathoms, quoted suggest that this record might be regarded with suspicion. Found on soft mud, muddy sand or clay, sometimes fine sand or sand with shell.

Specimens of *P. tenuispinus* forma *tenuispinus* were collected from hauls on the Hebridean Slope from 523 m to 1000 m depth and one only from the North Feni Ridge area in 2000 m, whereas others with basally broadened rays conforming to Sladen's variety *platynota* were identified in the 'cold' area north of the Wyville Thomson Ridge, the Faroe-Shetland Channel in 1040 m and 1050 m depth. The five specimens from ES 87 (61°13′N, 03°59′W) ranged from R 35 mm to R 5·8 mm. In the smallest specimen however, the bivalved adambulacral pedicellariae are not developed.

Reproduction. The sexes are separate; maximum oocyte diameter is 800 µm, suggesting a non-pelagic possibly lecithotrophic or direct development (Pain, Tyler & Gage, 1982*b*).

Order **VALVATIDA**

Family **ODONTASTERIDAE**

Hoplaster spinosus Perrier, 1882

See: Perrier, 1894 : 324; Sladen, 1889 : 275 (as *Pentagonaster lepidus*).

Samples. AT 121 (3), AT 167 (1). [2910 m, 2300 m]

Distribution. Previously known from the vicinity of the Azores and in the Porcupine Seabight, recorded in an appendix by Mortensen 1927 : 439; 1800–2995 (?3307) m; soft mud or ooze.

The present records extend the known range north to 57°. The largest specimen, from the 2910 m haul, measured R 14 mm, whereas in the very few specimens previously described R did not exceed R 7·5 mm (Mortensen, 1927 : 77).

Remarks. The monotypic genus *Hoplaster* does not have the reflected hyaline-tipped oral spines otherwise characteristic of the family Odontasteridae but does show the distinctive odd interradial marginal plates.

Odontaster sp.

See: von Marenzeller, 1893 : 6, figs 4A–C (*Gnathaster mediterraneus*); Mortensen, 1927 : 77–78, figs 42, 43 (? *O. mediterraneus*); Verrill, 1899 : 206–207, pl. 29, fig. 3 (*O. hispidus*).

Sample. AT 162 (1). [992 m]

Remarks. The single (dried) specimen, from the N slope of the Porcupine Seabight, has R/r 29/11·5 mm = 2·5/1 and a relatively narrow frame of marginal plates. The Atlantic specimens recorded as *O. mediterraneus* by Koehler (1909) from the Bay of Biscay (*Princesse Alice* st. 1450, *c.* 45°N, 3°W, 1804 m, R 15 mm) and Mortensen (1927) from the Porcupine Seabight (*Helga,* 51°26′N, 11°45′W, 927 m, 'small'), as well as a record from the Seabight (unpublished, IOS st. 50601, 51°20′N, 11°42′W, 927 m, R/r 20/13 = 1·5/1), all have more nearly pentagonal form and disproportionally broad marginals, though this is probably at least partly attributable to the relatively small size. *Odontaster hispidus* Verrill, 1880 has only been recorded from the NW Atlantic in 73–1160 m. The body shape is very variable in *Odontaster* and the mean R/r ratio for both species is *c.* 2·5/1 in larger specimens, R > 20 mm. The main differences in mediterranean specimens appear to lie in broadened paxillar columns on the distal abactinal plates, frequent rather than occasional glassy 'crystal bodies' embedded in the distal superomarginals, both visible when the plates are denuded, short capitate superomarginal spinelets and three or four rather than two, occasionally three, furrow spines. The present specimen has the distal abactinals no broader than the proximal ones, no crystal bodies and tapering slender superomarginal spinelets. However, it does have four furrow spines on a few plates, otherwise three; also the actinal armament is less crowded than is usual in *hispidus,* though the dry condition may contribute to this. In the IOS specimen the abactinal areas are not at all prolonged on to the rays and the more distal plates still have round columns, there are no crystal bodies on the marginals and the furrow spines usually number three but the superomarginal armament is very short and slightly capitate. Clearly further material and comparison is needed for the specific identity of these specimens to be established.

Family **RADIASTERIDAE**

? Radiaster tizardi (Sladen, 1882)

See: Mortensen, 1927 : 97, fig. 55.

SAMPLE. ES 10 (juvenile, 1). [2540 m]

DISTRIBUTION. Although according to Mortensen (1927) this species is previously known only from the Faroe-Shetland Channel (*Triton* and *Knight Errant*) and the Porcupine Seabight (*Helga*) in 930 (? 730) m–1320 (? 1630) m, Sladen (1882) gives the single *Knight Errant* record as from 59°33 ′N, 07°14 ′W in 1015 m depth on the 'warm' side of the Wyville Thomson Ridge in the northern Rockall Trough; mud or ooze.

REMARKS. The single specimen measures R = 3·5 mm, r = 2·0 mm. The abactinal armament appears clustered and the margins thick. The present record must be uncertain in view of the small size of the specimen, specimens of *tizardi* are not yet known with R < *c.* 60 mm, and the considerable depth (2540 m) from which it was collected.

Family **GONIASTERIDAE**

Pseudarchaster parelii (Düben & Koren, 1846)

See: Süssbach & Breckner, 1911 : 202–203 (as *Tethyaster parelii*); Mortensen, 1927 : 87–88, fig. 49; Halpern, 1972 : 366–370.

SAMPLES. ES 55 (? [juveniles] 9), ES 56 (? [juveniles] 2), ES 87 (? [juvenile] 1), AT 114 (1), AT 132 (1), AT 138 (1), AT 139 (2), AT 144 (1), AT 151 (1), AT 154 (1), AT 167 (1), AT 175 (1), ES 176 (1), AT 177 (2), AT 181 (1), ES 184 (1), AT 191 (10), AT 192 (1), AT 195 (2), AT 198 (juvenile, 1), ES 200 (1). GT 1 (2), GT 7 (2), GT 13 (1), GT 14 (2), SWT 10 (2), SWT 11 (1), SWT 16 (4), SWT 17 (1), SWT 18 (8), SWT 27 (1). [225–2965 m]

DISTRIBUTION. Previously known from Greenland south to the West Indies in the western Atlantic, and from northern Norway to the Bay of Biscay and the Azores in the east; 15–3000 m, southern records being from deep water; preferring waters with a temperature slightly above zero (D'yakonov, 1950) or from 4–8°C (Cherbonnier & Sibuet, 1973) and 1·5–6°C (Halpern, 1972); on bottoms of soft mud to sand, sometimes with pebbles (D'yakanov. 1950).

Our present records from the Rockall Trough range from 225 m on the Porcupine Bank to 2965 m in the vicinity of the Permanent Station, where juveniles only were collected, and hence apparently show an ability to tolerate temperatures from 2 to 5°C up to *c.* 9·5–10°C from hydrographic data in Ellett & Martin (1973).

REPRODUCTION. Preliminary examination of the gonads of some of these specimens indicates that the sexes are separate, while the presence of large oocytes (*c.* 1000 μm) suggests direct or demersal development (Tyler, Pain & Gage, 1982*b*; Tyler & Pain, 1982*b*).

REMARKS. The colour of fresh specimens was a rose pink; Mortensen (1927) and D'yakonov (1950) describe freshly collected specimens as bright red to red-brown on the dorsal side.

Pseudarchaster gracilis (Sladen, 1889)

See: Halpen, 1972 : 360–366, figs 1, 2; Downey, 1973 : 59–60, pl. 23, figs C, D.

SAMPLE. SWT 18 (1). [1785–1845 m]

DISTRIBUTION. Previously known from just south of Cape Cod and from the Gulf of Mexico to Surinam, in the W Atlantic; from the Azores and from Mauritania to the Gulf of Guinea in the east; 320–2736 m. (Only in the West Indies area from < 1000 m).

This record on the Hebridean slope extends the known distribution of *P. gracilis* to British waters. Although it is known to occur on both sides of the North Atlantic, the most northerly of previous records in the east were from the Azores.

Paragonaster subtilis (Perrier, 1881)

See: Halpern, 1972 : 374–378, figs 5 (pt), 6 (pt); Downey, 1973 : 57, pl. 22, figs A, B.

SAMPLES. ES 6 (juvenile, 1), ES 27 (1), ES 28 (2), ES 34 (1), ES 53 (2), ES 56 (1), ES 111 (1), AT 121 (17), ES 129 (2), AT 131 (2), AT 138 (1), AT 139 (1), ES 140 (2; ? [juvenile] 1), AT 141 (6), ES 147 (1), ES 164 (1), AT 171 (juveniles, 2), AT 177 (juvenile, 1), ES 180 (3), AT 186 (5). SWT 16 (17), SWT 17 (5), SWT 18 (4), OTSB 51001 (1). [1785–1845 m to 2925 m]

DISTRIBUTION. Previously known from south of Cape Cod and the Gulf of Mexico, in the W Atlantic, the Azores and mid-equatorial Atlantic, and from the Bay of Biscay, C. Verde Is. area and Gulf of Guinea in the east; 2455–4700 m; soft ooze. This N Atlantic species has an abyssal distribution not previously known to extend further north than Biscay in the NE Atlantic.

The present records, although mostly from the vicinity of the Permanent Station (*c.* 2900 m depth) confirm the essentially abyssal distribution of *P. subtilis,* although the shallowest record of 1785–1845 m from 56°46′N on the Hebridean slope is less than the minimum depth of 2455 m quoted by Halpern (1972). The temperature range quoted by Halpern is 1·5–4°C.

REPRODUCTION. The sexes are separate with a maximum egg size of about 1000 μm in females, suggesting direct development (Tyler, Pain & Gage, 1982*b*; Tyler & Pain, 1982*b*).

Plinthaster dentatus (Perrier, 1884)

See: Halpern, 1970 : 244–252, figs 17, 18, 19; Downey, 1973 : 52–53, pl. 19, figs A, B.

SAMPLES. ES 59 (juvenile, 1), AT 68A (2), ES 169 (juvenile, 1), ES 185 (juvenile, 1) SWT 18 (1). [1331–2190 m]

DISTRIBUTION. Previously known from both sides of the north and central Atlantic, from North Carolina to northern Brazil in the west and from the west of Ireland to Liberia in the east and from the Azores; 229–2117 m; on muddy sediments.

Although previously collected in the Porcupine Seabight (Farran, 1913; Grieg, 1921), the present records extend the known northward distribution of this N Atlantic species to latitude 59° and extend the lower limit of its depth range from 1804 m (Halpern, 1970) in the eastern Atlantic to 2910 m.

Evoplosoma scorpio Downey, 1981

See: Downey, 1981 : 561–563, fig. 1.

SAMPLE. ES 112 (3). [1900 m]

DISTRIBUTION. Previously only known from the holotype taken by the *Sarsia* off the Western Approaches to the English Channel (*c.* 48°N, 10°W); *c.* 1600 m (Downey, 1981).

The new record provides a northward extension of range to the Feni Ridge in Rockall Trough. Two other species of *Evoplosoma* are known, one from the Pacific near Hawaii, the other south of Sri Lanka in the Indian Ocean.

REMARKS. The present specimens are large and robust, R 90–130 mm, R/r 3·3–3·6/1.

Evoplosoma is closely related to *Hippasteria* but differs from *H. phrygiana* in the long narrow arms (R/r *c.* 3·5/1), continuous irregular granulation interspersed with conical spines and pedicellariae with the two valves elongate, projecting and spatuliform rather than extremely short but very broad and almost flush with the body surface, as in *Hippasteria.*

Family **PORANIIDAE**

Porania pulvillus (O. F. Müller, 1766)

See: Döderlein, 1900 : 217–218, pl. 8, figs 10, 10a; Süssbach & Breckner, 1911 : 218–219; Mortensen, 1927 : 90–92, fig. 51.

SAMPLES. ES 33 (1), ES 113 (1, juveniles, 2). [148 m, 168 m]

DISTRIBUTION. Previously known from Scandinavia, the Lousy Bank and west of Ireland south to the Bay of Biscay; 10–1000 m but rarely deeper than 300 m, on the usually mixed, sandy sediments of commercial trawling grounds.

The present records span the Rockall Trough and fall within the known bathymetric range although *P. pulvillus* apparently has not been previously recorded from Rockall Bank (ES 113).

REMARKS. The two small specimens (R *c.* 6·5 mm) from ES 113 resemble the holotype of *Marginaster fimbriatus* Sladen, 1889 from *Porcupine* st. 31, *c.* 56°N, 11°30′W, 2487 m, in the prominent inferomarginal fringe but have relatively sparse abactinal and actinal armament, only a single actinal spinelet in each interradius. *Marginaster fimbriatus* was referred to the synonymy of the Mediterranean *M. capreensis* (Gasco) by Ludwig, 1897 followed by Mortensen (1927) (see fig. 54) but A.M.C. believes it more likely to be the juvenile form of another poraniid from this vicinity. The large specimen from the same station, R 55 mm, is unusual in having the inferomarginal spines mostly aborted, there being only one or sometimes two on five to seven proximal plates of each interradial arc.

Order **SPINULOSIDA**

Family **PTERASTERIDAE**

Pteraster militaris (O. F. Müller, 1776)

See: Süssbach & Breckner, 1911 : 226; Mortensen, 1927 : 104–105, fig. 60.

SAMPLES. ES 87 (juveniles, 2). GT 2 (2), GT 11 (1). [934–1054 m to 1050 m]

DISTRIBUTION. This is an arctic-boreal species with a circumpolar distribution in the Arctic and a NW and NE Atlantic distribution along the American coast to Cape Cod, off the north west of Scotland and in the Faroe Channel, and off the entire west coast of Norway (D'yakonov, 1950); 10–1100 m.

The present records are all from around 1000 m and extend the known distribution slightly (and predictably) to the Rockall Trough.

Pteraster pulvillus M. Sars, 1861

See: Süssbach & Breckner, 1911 : 227; Mortensen, 1927 : 103; D'yakonov, 1950 : 81.

SAMPLES. ES 113 (juvenile, 1), ES 115 (? [juvenile] 1). [168 m, 1000 m]

DISTRIBUTION. This circumpolar N boreal species is known to range southward along the Atlantic coast of N America to 42°N (Massachusetts Bay and Bay of Fundy) and on the Norwegian coast down to 60°N in the vicinity of Bergen (D'yakonov, 1950). The record from Rockall Bank together with that recently recorded on the West Irish shelf in 122 m depth (O'Connor, 1981), confirm Mortensen's (1927) prediction that this species would be found in areas round the British Isles; 36–3700 m (2021 fms [= 3696 m] according to Sladen, 1889).

REMARKS. The specimen from ES 115 is in poor condition and has the stomach everted, damaging the oral furrow armament so that the characteristic continuous webbing of the oral furrow spines across the apex of each jaw has been ruptured, if it was present. The good specimen from ES 113 has R/r 8/6 mm.

Pteraster reductus Koehler, 1907

See: Koehler, 1909 : 96–97, pl. 3, figs 8, 9, pl. 20, figs 10; Grieg, 1921 : 28–29, pls 5, 6, 7; Mortensen, 1927 : 103.

SAMPLE. ES 112 (juvenile, 1). [1900 m]

DISTRIBUTION. This species is known only from the Azores and a single specimen from the South Feni Ridge in 2215 m (Cherbonnier & Sibuet, 1973); 1920–2900 m.

It is interesting that the present specimen was also collected from the Feni Ridge at a depth nearly within the previously recorded bathymetric range.

Pteraster sp. aff. ***P. acicula*** (Downey, 1973)

See: Downey, 1973 : 79, pl. 34, figs C, D.

SAMPLE. GT 16 (1). [958 m]

DISTRIBUTION. *P. acicula* has only been recorded from a few small poorly-preserved specimens (R up to 8 mm) from the northern Gulf of Mexico in 1060–1316 m, so the identification of the Rockall Trough specimen remains to be confirmed.

REMARKS. The complete absence of webbing from the oral furrow spines, characteristic of the subgenus *Apterodon,* and the very large number of paxillar spinelets (*c.* 25 on one midradial paxilla) distinguish this specimen from all the NE Atlantic Pterasters hitherto recorded.

HYMENASTER Wyville Thomson

At present there is some confusion over the taxonomy of *Hymenaster* in the N Atlantic. We here retain the specific names *membranaceus, pellucidus, gennaeus* and *rex* according to the original identifications of the specimens made from Sibuet's tabular key to the Atlantic species (1976), pending a forthcoming comprehensive review of the family by M. E. Downey, in Clark & Downey (in prep.). A.M.C. dissociates herself from the identification of N Atlantic specimens as *H. gennaeus,* believing that Sibuet (1976) had a mistaken concept of *H. giganteus* as a membranous rather than a fleshy species as Farran (1913) describes the type and *Helga* specimens.

Hymenaster membranaceus Wyville Thomson

See: Sladen, 1889 : 521–2, pl. 92, figs 6, 7, pl. 93, figs 10–12; Mortensen, 1927 : 106; Sibuet, 1976 : 315–318, fig. 6 A, B.

SAMPLES. ES 12 (2), AT 141 (juvenile, 1), AT 144 (287), AT 151 (30), AT 153 (203), AT 154 (111), AT 161 (3), AT 167 (137), AT 171 (556), AT 175 (180), ES 176 (60), AT 177 (319), AT 181 (354), ES 182 (16), ES 184 (79), AT 186 (423), AT 191 (? [juveniles] 47), AT 195 (410), ES 197 (37), AT 198 (133), ES 200 (15; ? [juveniles] 4). SWT 32 (1). [1995–2020 m to 2909 m]

DISTRIBUTION. Known from the E, N and S Atlantic from a depth range of 1000–3000 m; on soft ooze. Results of recent intensive sampling in the Bay of Biscay indicate a somewhat restricted bathymetric range (2119–2878 m, Sibuet, 1976).

H. membranaceus was collected in large numbers from St. 'M' (*c.* 2200 m depth), apart from a single juvenile specimen from the Permanent Station (2909 m), a sample of three from the Porcupine Seabight (*c.* 2055 m) and two records (2; 1 specimen) from the Barra Fan in the northern Rockall Trough (2076 m; 1995–2020 m).

Reproduction. The eggs of this species grow to 1100 µm diameter, suggesting direct development (Pain, Tyler & Gage, 1982*a*). These authors also indicate that there is no synchrony in gametogenic development in the population, and that breeding probably occurs year-round at a low level. Size frequency data from St. 'M' suggest a low possibly continuous recruitment to the population which consists mainly of mature adults. The sexes are separate and, although fertilization may take place in the supradorsal chamber, there is no evidence of brooding in the St. 'M' population.

Remarks. *H. membranaceus* is thought to live partially buried in bottom sediment, with only the valves of the central opening protruding above the sediment in order to allow ventilation of the supradorsal cavity (Mortensen, 1927). However, we note here that in photographs of the bottom in the Porcupine Seabight in Rice *et al.* (1982), specimens of '*Hymenaster* sp.', that are probably the same as the present species, are shown lying on the sediment surface. Possibly these animals were in the process of changing station where they would normally be buried out of sight.

Hymenaster pellucidus Wyville Thomson, 1873

See: Danielssen & Koren, 1884 : 72–80, pl. 13, figs 1–17, pl. 15, figs 7–8; Grieg, 1921 [1932]: 29; Mortensen, 1927: 107– 108, figs 62, 63 1, 2.

Sample. ES 87 (1). [1050 m]

Distribution. Previously known from the Siberian and Norwegian Seas, extending to the Faroe Channel in *c.* 15–2800 m.

This very delicate, perfect specimen, R 22 r 15 mm, R/r 1·5/1, is from the Faroe-Shetland Channel.

Hymenaster gennaeus H. L. Clark, 1923

See: H. L. Clark, 1923 : 302–303, pl. 10; Sibuet, 1976 : 311–314, figs 4, 5B.

Samples. AT 144 (1), AT 154 (1), AT 171 (1), AT 181 (1), AT 195 (? 1). SWT 11 (1). [2190 m to 2500–2560 m]

Distribution. Known previously only from the holotype (Clark, 1923) taken by *Pieter Faure* in the SE Atlantic near Cape Point in 1400 m and one specimen from *c.* 47°35′N, 8°39′W in 2245 m (Sibuet, 1976) but see note on p. 282.

Our records are from St. 'M' *c.* 2200 m, except for one specimen from 2500–2560 m at *c.* 56°N, 11°W that was taken in a fish trawl.

Remarks. The queried specimen from AT 195 is probably not conspecific with the rest, having a subpentagonal rather than pentagonal body form, R/r nearer 2/1 than 1·5/1, consistently single paxillar spines rather than usually three, but three rather than usually one, sometimes two adambulacral spines. It agrees better in these characters with *H. regalis* Verrill, 1895, known from Carolina to Cuba, but that species is supposed to lack the smooth interbrachial arcs found in this specimen.

Reproduction. Preliminary observations of Pain, Tyler & Gage (1982*a*) indicate an egg size and mode of development similar to that of *H. membranaceus.*

Hymenaster rex Perrier, 1894

See: Perrier, 1894 : 186–189, pl. 13, fig 2; Grieg, 1921 [1932]: 29–30.

Sample. AT 121 (1). [2910 m]

Distribution. Previously known from the Bay of Biscay (*c.* 46°N, 07°W) south to off NW Africa, 1140–2285 m, so the present record provides extensions northwards and downwards.

Remarks. This specimen has R/r 11/8·5 mm, the form being almost pentagonal. There are 3 adambulacral and oral furrow spines and 2 suboral spines on each plate.

Family **SOLASTERIDAE**

Crossaster squamatus (Döderlein, 1900)

See: Döderlein, 1900: 208–209, pl. 6, figs 5–5c (*as Solaster papposus* var. *squamata*); Greig, 1921 [1932]: 26–27 (as *Solaster squamatus*); Mortensen, 1927: 114 (as *S. squamatus*).

Sample. ES 87 (9). [1050 m]

Distribution. Known from west of Greenland to the Barents Sea, including most of the cold area of the Norwegian Sea south to the Faroe Channel (*c*. 61°N, 4°30′W, *M. Sars*); 100–1600 m. Previous records from the Faroe Channel area are all *c*. 1000 m.

Family **ECHINASTERIDAE**

HENRICIA Gray

The treatment of the genus *Henricia* provisionally follows Mortensen (1927) pending further study by A.M.C. in Clark & Downey (in prep.).

Henricia sanguinolenta (O. F. Müller, 1776)

See: Süssbach & Breckner, 1911 : 224–226 (as *Cribrella sanguinolenta*); Mortensen, 1927 : 118–120, fig. 70.

Sample. ES 23 (1). [704 m]

Distribution. Owing to confusion about the specific limits, it is impossible to give a precise range. *Henricia sanguinolenta* sensu stricto appears to range from the north east of the U.S.A. to Iceland, the Faroes, northern British Isles, Scandinavia and the White Sea in depths possibly from *c*. 10–1000 m.

The present record (R/r 57/13 mm) of this coastal species is from the Hebridean Slope.

Henricia abyssicola (Norman, 1869)

See: Mortensen, 1927 : 120–121, fig. 71.

Samples. ES 99 (2), ES 112 (juvenile, 1), ES 113 (juvenile, 1). [168–1900 m]

Distribution. Previously recorded off SW Ireland (*Helga*) and from the 'warm' area of the Faroe Channel (*Triton*) in *c*. 930–1400 m.

The present records lie at widely varying localities and depths; two are from within the Rockall Trough, while one is from Rockall Bank (ES 113). They are considerably shallower than previous records of this species, which is apparently not recorded from localities other than off the British Isles.

Order **FORCIPULATIDA**

Family **BRISINGIDAE**

Brisinga endecacnemos Asbjörnsen, 1856

See: Farran, 1913 : 27–28; Mortensen, 1927 : 125–127, fig. 73.

Samples. AT 107A (1), AT 151 (1), AT 181 (1), AT 186 (8), AT 192 (14), ES 200 (2). SWT 17 (12), SWT 18 (1), SWT 32 (13). [1785–1845 m to 2220 m]

Distribution. Previously recorded from the Faroe Channel and southern Norway, south to the Cape Verde area and from the Porcupine Seabight, the last by Farran (1913); 286–2200 m.

Feeding. Bottom photographs and submersible observations have led to speculation on the mode of life of members of this very singular deep-sea family. A bottom photograph in Rowe & Staresinic (1979) from the Tongue-of-the-Ocean (Bahama Is.) at 2000 m shows an asteroid (with arms raised up in a filter feeding posture) which probably belongs to this family. Pawson (1978) gives photographs of brisingids in a similar posture and comments that they are presumably capturing particulate matter from the water and transporting it to the mouth by ciliary currents.

REPRODUCTION. The oocytes grow up to 1250 μm in diameter (P.A.T., personal observations); this suggests a direct mode of reproductive development.

REMARKS. This species is thought to prefer a rocky bottom (Mortensen, 1927). Some of the present records of this very large species are of disks only. This is unfortunate, as the serial gonads in the arms of *Brisinga endecacnemos* provide the most obvious distinguishing feature from *Brisingella coronata.*

Brisingella coronata (G. O. Sars, 1871)

See: Ludwig, 1897 : 418; Mortensen, 1927 : 127.

SAMPLES. AT 138 (1), AT 162 (5), AT 167 (4), ES 176 (1), AT 177 (1). [992–2450 m]

DISTRIBUTION. Recorded from the Rockall Trough by Grieg (1921) and off northern Norway south to the Cape Verde Is. area and the Azores; 100–2600 m.

The present records at 992 m in the Porcupine Seabight, where it has previously been collected by Farran (1913), and at St. 'M' hence are not unexpected.

REPRODUCTION. The eggs grow up to 1200 μm diameter (P.A.T., personal observations); this suggests direct development.

Freyella spinosa Perrier, 1894

See: Perrier, 1894 : 85–89, pl. 8; Mortensen, 1927 : 129.

SAMPLE. SWT 15 (6). [4810 m]

DISTRIBUTION. Previously known from the Bay of Biscay south to the Azores and Angola; 1884–4060 m.

The present record extends the range northwards into the Porcupine Abyssal Plain and downwards to 4810 m depth.

REMARKS. Pawson (1978) mentions that he has observed from the submersible *Alvin* a species of *Freyella* feeding with '. . . arms upraised, and it tends to raise itself as far as it can into the water column by climbing to the tops of nearby rocks.'

The stronger articulation at the base of each arm ensures that most specimens of *Freyella* are preserved with at least the proximal parts of some arms still attached to the disk, unlike *Brisinga* and *Brisingella. F. spinosa* has 8–13 arms.

Freyella sexradiata (Perrier, 1885)

See: Perrier, 1894 : 89–90, pl. 3, fig. 2; Grieg, 1921 [1932]; 30–31, fig. 10; Mortensen, 1927 : 129.

SAMPLE. SWT 15 (1). [4810 m]

DISTRIBUTION. Previously recorded from the Bay of Biscay south to the latitude of Gibraltar (*c.* 35°N) and west to the Azores; 4020–5110 m.

The single specimen collected in the Porcupine Abyssal Plain along with *F. spinosa* likewise extends the known range northwards from the Bay of Biscay.

Family **ASTERIIDAE**

Hydrasterias sexradiata (Perrier, 1882)

See: Perrier, 1894 : 100–102, pl. 9, fig. 2 (as *Pedicellaster sexradiatus*).

SAMPLES. AT 138 (arms), AT 139 (arms), AT 154 (7), AT 167 (1), ES 176 (juvenile, 1). [2245–2450 m]

DISTRIBUTION. Previously known from the Bay of Biscay south to the Cape Verde Is. area and the Azores; 600–4260 m.

This record extends the known distribution of this species northward in the NE Atlantic to the Rockall Trough.

ONTOGENY. The juvenile specimen is at the armless 'Stellosphaera mirabilis' stage of Perrier (1894). The identification has been confirmed by Miss M. E. Downey of the Smithsonian Institution, Washington, U.S.A., partly on the basis of the structure of the crossed pedicellariae, which are much more compact than those of *Freyella sexradiata*, the only other six-rayed forcipulate known from this vicinity.

Stichastrella rosea (O. F. Müller, 1776)

See: Süssbach & Breckner, 1911 : 228–229 (as *Stichaster roseus*); Mortensen, 1927 : 136, fig. 77.

SAMPLES. ES 15 (1 var. *ambigua*), ES 33 (2), ES 113 (4; juvenile, 1). GT 1 (2 var. *ambigua*), GT 7 (1 var. *ambigua*), GT 14 (3). [168–1632 m]

DISTRIBUTION. Previously known from the Lofoten Is., Norway and the north and west of the British Isles south to the Bay of Biscay; 4–1150 (? 1330) m.

The present records are from the Hebridean Slope, adjacent shelf and the Rockall Bank and show a considerable depth range. Mortensen (1927) cites records of this species known only from the NE Atlantic from 4 m to 430 m depth, while in 586 (?–393) m–1146 (? 1331) m in the Porcupine Seabight Farran (1913) records a variety *ambigua* with shorter and stouter arms which differs also in the even more regular arrangement of the dorsal skeletal plates than is present in *S. rosea* sensu stricto, itself a relatively regular asteriid. On this account together with the bathymetric difference, A.M.C. considers that a specific rank for *ambigua* may prove to be more appropriate. The problem will be considered in Clark & Downey (in prep.).

REMARKS. The juvenile specimen from St. ES 113 has R only 3·9 mm, R/r 1·6/1. The relatively large semicircular terminal plates are 1·3 mm broad and each bears a conspicuous horizontal fan of fourteen flat petaloid spines similar to the two spines on each of three ambital inferomarginals in each series, the first inferomarginal being spineless and the fifth and distalmost with a single smaller spine.

Family **ZOROASTERIDAE**

Zoroaster fulgens Wyville Thomson, 1873

See: Farran, 1913: 19–22, pl. 1, fig. 3 (as *Z. fulgens* var. *Ackleyi*); Mortensen, 1927: 132–133, fig. 75.

SAMPLES. ES 10 (3), ES 18 (3), ES 20 (1), ES 34 (26), AT 107A (2), AT 114 (17), AT 138 (9), AT 139 (18), AT 171 (7), AT 175 (3), AT 177 (9), AT 181 (3), ES 182 (1), AT 186 (7), AT 191 (juveniles, 11), AT 192 (7), AT 195 (1). GT 17 (2), SWT 10 (1), SWT 11 (2), SWT 12 (1), SWT 13 (1), SWT 15 (1), SWT 16 (366), SWT 17 (128), SWT 18 (21), SWT 27 (2), AT 3 (2). [*c*. 1000–4810 m]

DISTRIBUTION. From its original discovery by the *Porcupine* in the N Rockall Trough in 1869 (W. Thomson, 1873), this species has been found from hauls on soft ooze all over the deep N Atlantic.

The deepest of the present records (SWT 15) from the Porcupine Abyssal Plain extends the previously known bathymetric range of 367–3660 m (Downey, 1973) to 4810 m. However, if *Z. longicauda* Perrier, 1885, from NW of Africa and the Azores, is conspecific with *Z. fulgens*, as Downey (1970) notes is probable, then the previously known depth range must be extended to 4255 m. Specimens were numerous in the vicinity of St. 'M' at depths around 2200 m. The shallowest station was on the adjacent Hebridean Slope.

A photograph showing *Z. fulgens* in situ on the bottom was taken during a RRS *Challenger* haul at *c.* 49°22′N, 12°49′W in 1398–1404 m depth (Rice *et al.*, 1982; fig. 2(e)).

Reproduction. *Z. fulgens* has a maximum egg size of 950 µm (P.A.T., personal observation).

Remarks. Specimens examined from St. 'M' occasionally contained one or more specimens of an unidentified species of the parasitic ascothoracid barnacle, *Dendrogaster* (P.A.T., personal observations).

Class **OPHIUROIDEA**

Suborder **EURYALIDA**

Family **ASTERONYCHIDAE**

Asteronyx loveni Müller & Troschel, 1842

See: Süssbach & Breckner, 1911 : 262; Mortensen, 1927 : 158–160, fig. 90; D'yakonov, 1954 : 21–22, fig. 4.

Samples. SWT 18 (1), SWT 32 (1). [1785–1845 m to 1995–2020 m]

Distribution. This is a widespread species found in all the major oceans except the Arctic; previously recorded bathymetric range, *c.* 100–2963 m. Mortensen (1927) lists several records around the coast of Scotland and Grieg (1921) took a specimen from the Porcupine Seabight at 1797 m.

The present specimens are from the Hebridean Slope and thus extend the known distribution into the Rockall Trough.

Remarks. The long prehensile arms and climbing habit on gorgonians and pennatulids is typical of euryalids. One specimen collected was entwined in characteristic posture around the pennatulid *Distichoptilum gracile* Verrill. Grassle, Sanders, Hessler, Rowe & McLellan (1975) observed *Asteronyx loveni* from the submersible *Alvin* at *c.* 1800 m depth off New England, the ophiuroid being present coiled in the branches of every gorgonian seen. Hartman (1963) photographed *A. loveni* on the ocean floor using its long arms to feed from the water column above. Mortensen (1927), in notes on the biology of this species, states that adults are plankton eaters; two or three arms are wound around the pennatulid, while the others wave freely in the water catching the small pelagic animals, mainly copepods, on which it feeds. Mortensen also thought that this species may feed on the polyps of the pennatulid to which it clings.

Astrodia tenuispina Verrill, 1884

See: Verrill, 1884 : 219; Koehler, 1907 : 304, pl. 21, figs 48–50.

Sample. SWT 13 (147). [3425–3500 m]

Distribution. Previously recorded from the N Atlantic deep-sea region; 2365–3300 m.

This unusually large sample was recovered from the deep water connecting the southern Rockall Trough with the Porcupine Abyssal Plain, so being the first record for this species in the deep sea around the British Isles and from a greater depth than previously recorded.

Remarks. Most specimens when examined were entwined around the pennatulid *Scleroptilum grandiflorum* Kölliker.

The stomach was devoid of recognisable contents except in one of ten individuals examined. In this specimen, remains of the uropods of a mysid crustacean were found. It seems likely that this species feeds on plankton in a manner similar to that which Mortensen (1927) supposed for *Asteronyx loveni.*

Reproduction. Measurements of disk diameter show a unimodal frequency ranging from 5·25–11·25 mm, peaking in the 7·50–7·75 size interval. Of the ten individuals dissected, all appeared to have female interradial gonads, each gonad containing mainly large yolky-looking eggs. Fecundity, expressed as the number of visible gonads, may vary widely between individuals. In one specimen, the gonads extended dorsally over the large stomach.

Family **ASTEROSCHEMATIDAE**

Asteroschema inornatum Koehler, 1906

See: Koehler, 1909 : 206, pl. 3, figs 46, 47.

Sample. ES 112 (1). [1900 m]

Distribution. Known only from the NE Atlantic deep sea; 1480 m (Mortensen, 1933 : 114).

The present record from the Feni Ridge extends the bathymetric and northern geographic range of this species.

Remarks. The single specimen was entwined in characteristic fashion on a gorgonian provisionally identified as *Paramuricea biscaya* Grasshoff, 1977.

Family **GORGONOCEPHALIDAE**

Gorgonocephalus caputmedusae (Linnaeus, 1758)

See: Mortensen, 1927 : 162–163, figs 91, 92.

Samples. GT (1), AT 3 (1). [972–1084 m]

Distribution. West of the British Isles this species has been recorded off Cornwall, off SW Ireland and Lousy Bank; 1116–1214 m. Elsewhere it is known from scattered localities all over the N Atlantic; full bathymetric range *c.* 150–1200 m.

The present samples were recorded from the Hebridean Slope west of Barra.

Remarks. The recovery of a single specimen entangled around a sounding line cast to 800 fathoms (1463 m) in Baffin Bay during Sir John Ross' attempt to find the North West Passage represents probably the first ever record of a deep-sea animal (Menzies, George & Rowe, 1973). *Gorgonocephalus caputmedusae* uses its branched arms to ensnare plankton. Mortensen (1927) records that it is often found aggregated on rocks in current-swept areas.

Suborder **OPHIURIDA**

Family **OPHIACANTHIDAE**

Ophiotrema alberti Koehler, 1896

See: Koehler, 1909 : 196–198, pl. 28, figs 1, 2.

Sample. AT 192 (2). [1862 m]

Distribution. Previously recorded only from deep water off the Azores and in the S Atlantic (Mortensen, 1927); 3785–4060 m.

The present record from the Feni Ridge is considerably shallower than any previous record for this species.

Remarks. The dorsal side of the disk was missing from both specimens and large orange-yellow gonads were visible.

Ophiomyces grandis Lyman, 1879

See: Lyman, 1879 : 46, pl. 14 figs 383–385; 1882 : 241–242, pl. 19 figs 13–15.

Sample. SBC 62 (3). [610 m]

Distribution. Previously recorded from off Tristan da Cunha (1800 m) and in the Bay of Biscay; 230–800 m.

These specimens were collected from the Hebridean Slope west of Barra. This is the first record of *O. grandis* off Britain and is a northern extension of its known previous range.

Remarks. The scarcity of occurrence may reflect a lack of sampling in the present programme at depths between 230–800 m where it may be expected (Cherbonnier & Sibuet, 1973).

Ophiacantha abyssicola G. O. Sars, 1871

See: Mortensen, 1927 : 194, fig. 105; 1933 : 23–24, fig. 9.

Samples. ES 23 (4), ES 115 (4; ? [juveniles] 6). [704–1000 m]

Distribution. This species is distributed throughout the N Atlantic. Although a wide bathymetric range, *c.* 35–3500 m, is quoted (Mortensen, 1933; see also D'yakonov, 1954 and Cherbonnier & Sibuet, 1973), it appears to be essentially an upper bathyal species extending into the shallow coastal areas of the Norwegian Sea. It has also been recorded on the Irish shelf off Eagle Island at a depth of 301 m (Farran, 1913). Samples providing unpublished records of *O. abyssicola* collected by the *Porcupine* from Rockall and SW Ireland are to be found in the British Museum (Natural History).

Ophiacantha abyssicola was recovered only from the Hebridean Slope off Barra and on the Hebridean Terrace Seamount but, like *Ophiomyces grandis,* the apparent rarity of this species in the samples may result from lack of sampling at favourable depths.

Ophiacantha bidentata (Retzius, 1805)

See: Mortensen, 1927 : 196, fig. 105; 1933 : 20–22, figs 6–8.

Samples. ES 10 (39), ES 12 (? 1), ES 34 (11), ES 55 (juvenile, 1), ES 56 (juveniles, 2), ES 69 (? [juveniles] 2), AT 107A (7), ES 112 (7), AT 121 (14), AT 139 (8), AT 141 (12), AT 144 (211), ES 147 (3), AT 151 (72), ES 152 (juvenile, 1), AT 153 (96), AT 154 (69), SBC 155 (juvenile, 1), AT 157 (2), ES 164 (?[juvenile] 1), AT 167 (264), AT 171 (168), ES 172 (juvenile, 1), AT 175 (85), ES 176 (10; ? [juveniles] 17), AT 177 (259), AT 181 (128), ES 184 (55), AT 186 (217), AT 191 (49), AT 192 (168), AT 195 (186), ES 197 (104), AT 198 (34), ES 200 (45). SWT 10 (1), SWT 11 (2), SWT 16 (1), SWT 18 (1), SWT 32 (14). [1330–2925 m]

Distribution. A widespread Arctic species the range of which extends into the N Atlantic. A large bathymetric range of 10–4500 m is quoted (Mortensen, 1933), but in the 'warm water' areas of the N Atlantic the bathymetric distribution is more restricted and it rarely occurs above 500 m.

Ophiacantha bidentata occurs abundantly in the Rockall Trough. Agassiz trawls from the Feni Ridge and from the repeat station St. 'M' at depths of 1900–2200 m have collected large numbers of this species. It was also recorded from the Porcupine Seabight at 1765 m depth by Farran (1913) under the name *O. hibernica.*

Remarks. *Ophiacantha bidentata* was collected with its arms typically entwined in the branches of the gorgonian *Acanella arbuscula* (Johnson), which occurs in abundance on the west and east sides of the Anton Dohrn Seamount. It was also found occasionally attached to the calcareous bases of both living and dead specimens of *Flabellum alabastrum* Moseley. Grassle, Saunders, Hessler, Rowe & McLellan (1975), observed an *Ophiacantha* sp. (either *O. bidentata, O. aculeata* or *O. simulans*) from the submersible *Alvin*, on rocks and small cobbles but not on the mud bottom, at *c.* 1800 m off New England. *Acanella* seems to occur on relatively current-swept bottoms on the continental margin where it may show a consistent orientation to the current direction (Laubier & Sibuet, 1979). At St. 'M', near-bottom currents may reach almost 50 cm/sec (Edelsten, 1980). Hence it seems likely that *Ophiacantha bidentata*, in common with other ophiacanthids, feeds on suspended material using arms held out into the current in a similar way to that described by Warner & Woodley (1975) for *Ophiothrix fragilis* (family Ophiotrichidae).

The colour of the arms of fresh specimens was not drab brownish as Mortensen (1927) describes, but a fresh salmon pink, while the disk was a similar colour and greyish green where the underlying large green-coloured stomach showed through.

REPRODUCTION. Studies on the breeding of this species show that the St. 'M' specimens are protandrous hermaphrodites with probably direct or abbreviated development, whereas re-examination of the shallow Arctic population, originally studied by Thorson (1936), confirms his finding that these individuals have separate sexes (Tyler & Gage, 1982*a*). A much needed revision of the genus *Ophiacantha* may well separate the N Atlantic deep-sea populations as a distinct species from the shallow Arctic populations.

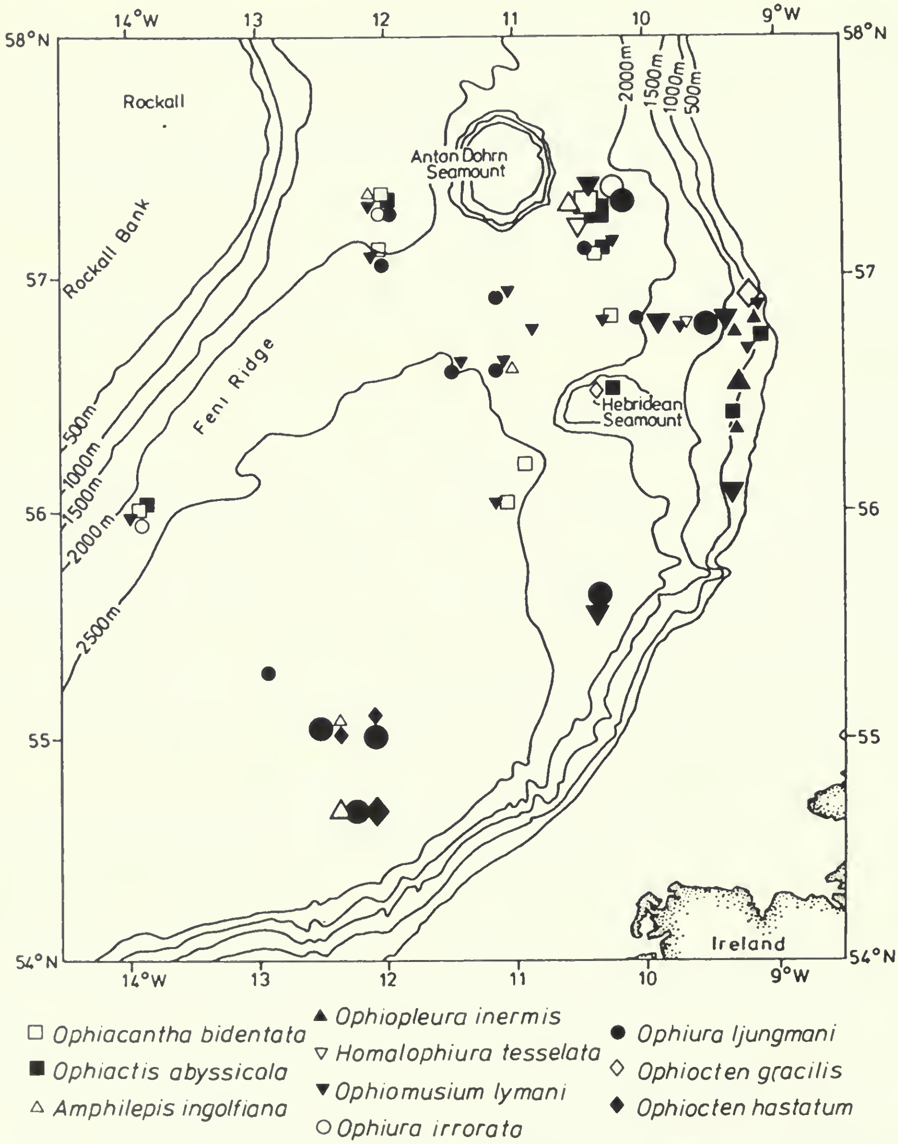
14°W
13
12
11
10
9°W
58°N
57
56
55
54°N
Rockall
Rockall Bank
Feni Ridge
Anton Dohrn Seamount
Hebridean Seamount
Ireland
500m
1000m
1500m
2000m
2500m
□ Ophiacantha bidentata
■ Ophiactis abyssicola
△ Amphilepis ingolfiana
▲ Ophiopleura inermis
▽ Homalophiura tesselata
▼ Ophiomusium lymani
○ Ophiura irrorata
● Ophiura ljungmani
◇ Ophiocten gracilis
◆ Ophiocten hastatum

Fig. 3 Chart of central part of Rockall Trough showing station locations for records of the ten most abundant brittle star species. Larger symbols denote records from more than one sample taken on or near the station position.

Ophiacantha crassidens Verrill, 1885

See: Mortensen, 1927 : 192–193, fig. 106.

Sample. AT 192 (6). [1862 m]

Distribution. Previously known only from the N Atlantic deep-sea region (Mortensen, 1933); *c.* 970–3120 m. This species was taken by the *Helga* in the upper Porcupine Seabight from 986 m to 1861 m depth (Farran, 1913) but was not previously known from the Feni Ridge where these specimens were collected in a single haul.

Remarks. The colour of fresh specimens is a pale yellowish pink with slightly greyish darker areas on the disk. The underlying stomach is orange coloured.

Ophiacantha cuspidata Lyman, 1878

See: Mortensen, 1933 : 31–33, figs 17, 18.

Sample. ES 112 (2). [1900 m]

Distribution. Previously known from scattered localities in the eastern and central North Atlantic from Iceland and off the Azores; 785–2460 m.

Two specimens were collected from the southern Feni Ridge making this the first record of *O. cuspidata* in the deep water off the British Isles.

Ophiacantha simulans Koehler, 1896

See: Mortensen, 1933 : 26–29, figs 11, 13.

Sample. ES 112 (26). [1900 m]

Distribution. Previously known in the eastern and central North Atlantic from off the Azores, the Bay of Biscay and S and SW of Iceland from 1480 m to 3018 m (Mortensen, 1933); in the western north Atlantic from off North Carolina.

The present record of twenty-six individuals from a single sled haul on the southern Feni Ridge represents an extension of the known range of this species to the British seas.

Remarks. It is interesting to note that an apparently discrete zonation of this species centred on 1900 m depth is described by Menzies, George & Rowe (1973) off the Carolinas (NW Atlantic). These authors also provide, from the basis of bottom photographs, a 'habitat sketch' of this animal lying on the sediment surface in a characteristic posture with the greater length of the arms raised vertically in the water, presumably feeding.

Ophiacantha aculeata Verrill, 1885

See: Mortensen, 1933 : 28–29, figs 14c, 15.

Sample. SWT 13 (1). [3425–3500 m]

Distribution. Previously recorded from the NW Atlantic with a bathymetric distribution of 2425–2510 m.

This solitary record from the Rockall Trough is the first from the E Atlantic and extends the bathymetric range.

Ophiolimna bairdi (Lyman, 1883)

See: Lyman, 1883: 256, pl. 5 (as *Ophiacantha*); Lütken & Mortensen, 1899; 177, pl. 18 (as *Ophiacantha*); D'yakanov, 1954 : 24, fig. 6.

Sample. ES 118 (1). [2910 m]

Distribution. *Ophiolimna bairdi* has a circumpolar arctic, N Atlantic and Pacific range; previously known bathymetric range 620–2600 m. The vertical limits of this species appear to be restricted in the warm water area of the N Atlantic to bathyal or abyssal depths and this species, like *O. bidentata,* seems to demonstrate Ekman's (1953) 'submergence' phenomenon.

This is the first record of this species in the Rockall Trough although Mortensen (1933) stated that this species can 'be expected to occur all over the deeper parts of the North Atlantic'.

Family **OPHIACTIDAE**

Ophiactis abyssicola (M. Sars, 1861)

See: Mortensen, 1933 : 47–50, figs 28–30.

SAMPLES. ES 18 (1), ES 34 (1), ES 112 (700), ES 113 (juvenile 1), ES 115 (7), AT 144 (2), AT 151 (1), AT 157 (43), AT 167 (3), AT 171 (2), AT 177 (9), ES 184 (2), AT 191 (16), AT 192 (26), AT 195 (9), ES 197 (1). GT 1 (3), GT 8 (1), SWT 12 (10), SWT 32 (2). [168 m to 2980–3000 m]

DISTRIBUTION. This species has a wide distribution throughout the Atlantic including the Norwegian Sea; 125–4000 m. *Ophiactis abyssicola* was previously taken in the Rockall Trough by the *Michael Sars* at 1856 m depth (Grieg, 1921).

Although occurring in small numbers in hauls from St. 'M', this species appears most abundant on the Feni Ridge from where in a single haul at 1900 m depth (ES 112) *O. abyssicola* dominated the ophiuroid catch. It also occurred in small numbers on the Hebridean slope as shallow as 650 m depth, and on the Hebridean Seamount at around 1000 m. Both locations are thought to be somewhat current-swept, as is also the area of the Feni Ridge sampled by ES 112 and the bottom at St. 'M'.

REMARKS. This species previously has been collected amongst branching corals and alcyonarians, and especially on the Bird's Nest Sponge, *Pheronema,* off western Ireland (Farran, 1913). The present records are mainly from St. 'M' where it was found entwined, along with *Ophiacantha bidentata,* amongst the bushy growths of the gorgonian *Acanella arbuscula.* It was occasionally also found in the base of both living and dead specimens of the solitary coral *Flabellum alabastrum.*

Freshly collected specimens are a fresh salmon-pink or orange colour, with grey colouring on the dorsal disk where the underlying stomach shows through the body wall.

Ophiactis balli (Thompson, 1840)

See: Süssbach & Breckner, 1911 : 252; Mortensen, 1927 : 200–202, fig. 112.

SAMPLE. ES 113 (1). [168 m]

DISTRIBUTION. Appears to be limited to the NE Atlantic where it has been recorded from both the Rockall and Lousy Banks, from off the south and west coasts of the British Isles and in the North Sea (Mortensen, 1927); mainly 60–400 m (extending to 1765 m). Farran (1913) lists records on the Porcupine Bank indicating that it is 'common . . . in water from about 30 fathoms downwards, wherever it can find crevices in stones or coral in which to insert itself'.

The present record on the Rockall Bank is not unexpected for this essentially upper bathyal-shelf species.

Family **AMPHIURIDAE**

Amphiura otteri Ljungman, 1871

See: Mortensen, 1933 : 59–61, fig. 35 (as *A. palmeri* Lyman).

SAMPLES. SBC 67 (1), ES 143 (1). [1000–2892 m]

DISTRIBUTION. This species is widespread, being found on both sides of the Atlantic; previously known bathymetric range, 210–1425 m.

These records from the Hebridean Slope and the Permanent Station appear to be the first published for this species from the deep sea around the British Isles, and the lower known depth range is extended.

REMARKS. The identification of this species was mistakenly given by Mortensen (1933) and Koehler (1907) as *A. palmeri* Lyman. Furthermore, we can find no difference between specimens described by Koehler (1896) as *A. grandis* and *A. otteri* Ljungman, 1871; *A. otteri* takes precedence.

Amphiura fragilis Verrill, 1885

See: Mortensen, 1927 : 214, fig. 121 (as *A. denticulata* Koehler).

SAMPLES. ABD 24 (2). [810 m]

DISTRIBUTION. *A. fragilis* has been recorded from both sides of the N Atlantic. In the west from off Martha's Vineyard north to the Davis Strait and W. Greenland. From the east it has been recorded from the Faroe Channel; 430–2640 m.

This sample is from the Hebridean Slope and is the first record of this species from the 'warm' water off the west of the British Isles.

Amphiura griegi Mortensen, 1920

See: Mortensen, 1927 : 210, fig. 119.

SAMPLE. ABD 24(1). [810 m]

DISTRIBUTION. Previously known from Norwegian fjords at 60 m to 300 m depth (Mortensen, 1920) and from the Bay of Biscay at 328–562 m (Cherbonnier, 1969; 1970). *Amphiura griegi* appears to be sporadically distributed from Norway south to the Bay of Biscay.

The present record of this little known species from the Hebridean Slope represents an interesting addition to its known geographic and bathymetric range.

Amphipholis squamata (Delle Chiaje, 1828)

See: Süssbach & Breckner, 1911: 253 (as *Amphiura elegans*); Mortensen, 1927: 221–222, fig. 125; A. M. Clark, 1970a: 30.

SAMPLES. ES 5 (5), ES 23 (juvenile, 2), SBC 66 (juveniles, 5), ES 99 (juveniles, 28), ES 115 (juvenile, 1), SBC 155 (juvenile, 1). [704–1330 m]

DISTRIBUTION. This species is known to have a cosmopolitan distribution throughout temperate and tropical coastal waters, which extends into the intertidal in the British Isles (Mortensen, 1927; Marine Biological Association, 1957); previously known from 0–809 m (Mortensen, 1933; Hartman & Barnard, 1958).

The present records on the Hebridean Slope, N Feni Ridge and Whittard Canyon considerably extend the lower limit of the previously known bathymetric range.

REMARKS. The microphagous suspension feeding mechanism of this species has been described by Pentreath (1970) from New Zealand material.

REPRODUCTION. *A. squamata* is known to brood its young (Mortensen, 1927; Fell, 1946) and hence it is difficult to explain the occurrence of individuals in deep water as sterile outliers resulting from fall-out of pelagic larvae emanating from shallower depths. We therefore infer a possibly continuous distribution from the intertidal zone (Loch Creran, personal observations of J.D.G.) to bathyal depths off the west of Scotland and probably elsewhere.

Subfamily **AMPHILEPIDINAE**

Amphilepis ingolfiana (Mortensen, 1933)

See: Mortensen, 1933 : 54–56, figs 31–33.

SAMPLES. ES 4 (134), ES 6 (10), ES 8 (1), ES 10 (29, ? 10), ES 12 (juvenile, 5), ES 27 (? [juveniles] 2), ES 32 (1), ES 34 (17), ES 55 (? 1), ES 56 (2), ES 111 (1), ES 118 (1), AT 121 (2), ES 135 (1), ES 140 (4), ES 143 (2), AT 151 (1), AT 153 (2), SBC 163 (1), ES 164 (2), ES 169 (juveniles, 3), ES 172 (juveniles, 5), ES 176 (18; ? [juveniles] 5), AT 177 (4), ES 180 (1), ES 184 (13), ES 185 (12), AT 186 (1), ES 190 (5), AT 192 (1), ES 197 (7, ? 1), ES 220 (1). [1862–2925 m]

DISTRIBUTION. Although Mortensen (1933) pointed out that the published records and descriptions of *A. norvegica* from the Atlantic (Lyman, 1882; Verrill, 1884; Koehler, 1924) refer to *A. ingolfiana*, it is likely that N Atlantic deep-sea records of *A. norvegica* made subsequent to publication of Mortensen's description of *A. ingolfiana* also should be referred to this species, notably those of Cherbonnier & Sibuet (1973) from the Bay of Biscay down to 4760 m depth.

Amphilepis norvegica then remains as an essentially shallow Arctic species with records from the northern Norwegian Sea down to the southern North Sea (Süssbach & Breckner, 1911) and the Faroe-Shetland Channel.

Amphilepis ingolfiana is probably widely distributed throughout the N Atlantic (see also Schoener, 1967) but because of the confusion existing between the two species, it is difficult to give an accurate geographic or bathymetric range. Mortensen (1933) quoted the depth range of *A. ingolfiana* as 957 to 2580 m.

REMARKS. Some specimens collected in our samples had a ferruginous staining that is often found on tubes or hard parts of burrowing fauna that generate a ventilatory current to their burrow. It is interesting to note that such currents have been observed in burrows of other amphiurid species (Woodley, 1975; Ockelmann & Muus, 1978).

Mortensen (1927) mentions that *Amphilepis norvegica* lives '. . . probably burrowed in the mud in the same way as the Amphiuras.' However, it seems unlikely that *A. ingolfiana* is a deep burrower in deep-sea sediments or else it would not be collected in Agassiz trawls or epibenthic sled hauls which disturb only the superficial sediment (Gage, 1975; Gage *et al.*, 1980). Barham, Ayer & Boyce (1967) observed and photographed a small ophiuroid, which they referred to as *Amphilepis* sp., from the bathyscaphe *Trieste* in the San Diego Trough at 1234 m depth: they describe it as normally buried '. . . with only its thin, sediment-colored rays splayed out on the surface.'

By analogy with Woodley's (1975) observations on five species of coastal amphiurids, it seems highly possible that *Amphilepis* is a shallow-burrowing deposit feeder, using the arms and tube feet as undulatory pumps that create a ventilating current, thus carrying mucus-trapped food particles from the tips to the mouth.

Schoener (1967) describes the morphology of the post-larvae and subsequent juvenile stages of this species, which would appear to have a widespread distribution in the N Atlantic deep sea (Mortensen, 1933).

Family **OPHIOCHITONIDAE**

Ophiochiton ternispinus Lyman, 1883

See: Lyman, 1883 : 255, pl. 5, figs 67–69; Mortensen, 1933 : 67–69, fig. 40, pl. 3, figs 25–26.

SAMPLES. AT 157 (2), AT 177 (1), AT 191 (1), AT 192 (1). SWT 18 (1). [1752–2200 m]

DISTRIBUTION. Previously recorded from the Faroes, W Ireland and N America; 425–1850 (? [2220) m. Mortensen (1933) considers that this large species probably is widely distributed in the N Atlantic deep sea. However, it seems likely that nowhere is it abundant, previous records being of single specimens in trawl hauls. The original description of Lyman (1883) was based on a specimen dredged by the *Porcupine* in the Porcupine Seabight. Grieg (1921) records a single specimen collected by the *Michael Sars* from a position in the Rockall Trough close to St. 'M'.

The present records extend the known deeper bathymetric range, although records for *O. grandis* Verrill, 1884, which Mortensen (1933) synonymises with *O. ternispinus,* and for *O.*

solutus Koehler 1907, which Mortensen (1927) considers may well represent the present species, extend the previous known range to 2220 m depth.

Remarks. The colour of fresh material was a drab olive on the disk with fawn coloured arms.

Family **OPHIURIDAE**

Subfamily **OPHIURINAE**

Ophiopleura inermis (Lyman, 1878)

See: Mortensen, 1927 : 251–252, fig. 137 (as *O. aurantiaca* (Verrill)).

Samples. ES 20 (1), ES 99 (1). GT 1 (3), GT 2 (1), GT 8 (5), GT 11 (1), GT 16 (6). [650–805 m to 1271 m]

Distribution. On comparing the syntypes of *Ophiura inermis* (Lyman) with specimens of *Ophiopleura aurantiaca* held in the collections of the British Museum (Natural History), we can find no difference between them. We therefore agree with Mortensen (1933) that the two names are synonymous, the species being distributed in both the N and S Atlantic with a bathymetric range of 280–1875 m. In the NE Atlantic, this species has been collected from depths of 567 m and greater off Iceland and around 1000 m depth in the N Rockall Trough (Hoyle, 1884) to *c.* 1200 m in the Porcupine Seabight and 1490–1740 m in the Bay of Biscay and the Azores (Mortensen, 1927).

The present records may reflect an intermediate level of progressive submergence in the range of this species from high to lower latitudes in the N Atlantic.

Ophiopleura borealis Danielssen & Koren, 1877

See: Mortensen, 1927 : 249–250, fig. 136; 1933 : 94–96.

Sample. ES 87 (4). [1050 m]

Distribution. Known previously from Arctic seas and off Britain from the cold area of the Faroe Channel; 10–1885 m.

The occurrence of this impressively large species amongst the present records is confined to a single haul from the cold water to the north of the Wyville Thomson Ridge.

Remarks. The four specimens collected measured from 33 to 35 mm in disk diameter (cf. the size frequency distribution in Mortensen (1933)).

Homalophiura tesselata (Verrill, 1894)

See: Koehler, 1898 : 37, pl. 7, figs 34, 36; 1909 : 156, pl. 25, figs 12–13; Mortensen, 1927 : 231–232.

Samples. AT 144 (2), AT 151 (1), AT 154 (2), AT 171 (3), ES 176 (1), AT 181 (1), ES 184 (1). SWT 18 (4). [1785–1845 m to 2264 m]

Distribution. *H. tesselata* has previously been found throughout the N Atlantic; 458–3720 m.

The present records, which extend the distribution of this species to the Rockall Trough, are all from St. 'M' (*c.* 2200 m depth) or the adjacent Hebridean Slope and lie within the bathymetric range quoted (Mortensen, 1927). *H. tesselata* remains unknown beyond the N. Atlantic (Cherbonnier & Sibuet, 1973).

Amphiophiura convexa (Lyman, 1878)

See: Lyman, 1878 : 84, pl. 3, figs 83, 84; 83, pl. 3, figs 85, 86 (as *A. bullata*); Mortensen, 1927 : 231.

Samples. ABD 3 (juvenile, 1), ES 10 (10). [1997–2540 m]

Distribution. This species may have a cosmopolitan distribution in the abyssal of the world ocean; 2160–5280 m in Atlantic (Cherbonnier & Sibuet, 1973).

REMARKS. Specimens were collected from two stations in the Rockall Trough. Cherbonnier & Sibuet (1973) found specimens possessing certain characteristics of both *A. convexa* and *A. bullata* (Wyville Thomson, 1873) suggesting that these are conspecific; they note that both have a nearly identical distribution in the Atlantic. *Amphiophiura convexa* was first recorded in the Pacific.

Amphiophiura saurura (Verrill, 1894)

See: Koehler, 1898 : 40, pl. 6, figs 19–21; Mortensen, 1927 : 231; 1933 : fig. 49, pl. 3, figs 9, 10.

SAMPLE. ES 112 (11). [1900 m]

DISTRIBUTION. Previously collected in the Bay of Biscay but unknown in British Seas. Although apparently uncommon, Mortensen (1933) suggests that this species has a wide distribution in the N Atlantic deep sea; 848–2167 m. The depth of the present record on the Feni Ridge falls within this range.

? Stegophiura macrartha H. L. Clark, 1915

See: H. L. Clark, 1915 : 315, pl. 19, fig. 7, 8.

SAMPLE. ES 112 (1). [1900 m]

DISTRIBUTION. Previously recorded only once before off Georgia (NW Atlantic) at a depth of 424 m.

This find on the Feni Ridge represents the first record in the eastern Atlantic and extends the bathymetric range to 1900 m.

Ophiocten gracilis (G. O. Sars, 1871)

See: Paterson, Tyler & Gage, 1982: 115–117.

SAMPLES. ES 4 (juveniles, 3315), ES 5 (juveniles, 265), ES 10 (juveniles, 43400), ES 12 (juveniles, 1240), ES 18 (juveniles, 4441), ES 20 (7465), ES 22 (6761), ES 23 (5665), ES 27 (juveniles, 3), SBC 46 (juveniles 3), ES 54 (juvenile, 1), SBC 58 (juveniles, 33), ES 59 (juveniles, 2281), SBC 60 (? [juvenile) 1), SBC 64 (juvenile, 1), SBC 65 (juveniles, 21), SBC 66 (57), SBC 67 (26), SBC 68 (juveniles, 11), ES 69 (9946), ES 90 (10), AT 90A (1), ES 111 (juvenile, 1), ES 99 (? 6; juveniles, 1627), ES 111 (juvenile, 1), ES 115 (312), ES 129 (juveniles, 5), ES 135 (juveniles, 16562), ES 137 (juveniles, 35), AT 141 (2), ES 147 (juveniles, 10263), ES 164 (juveniles, 417), ES 169 (juvenile, 1), ES 172 (juveniles, 1694), ES 176 (juveniles, 10380), ES 178 (147), ES 180 (juveniles, 8), ES 184 (juveniles, 650), AT 1 (77). [704–2925 m]

DISTRIBUTION. The synonomy and status of species of the genus *Ophiocten* have recently been revised by Paterson, Tyler & Gage, (1982). Identifications of populations of *O. gracilis* previously have been confused both with the shallow arctic species *O. sericeum* (Forbes) and with *O. abyssicolum* (Forbes) which is re-defined as a lusitanian species, the Atlantic distribution of which becomes increasingly submerged northwards, and does not appear to extend into the Rockall Trough (Paterson *et al.,* 1982).

We have found adults (2·50–4·75 mm disk) of *O. gracilis* only from upper bathyal depths on the Hebridean slope (stations ES 20, ES 22, ES 23, SBC 66, SBC 67 in the north Rockall Trough at 1040 m depth (ES 90) and on the Hebridean Seamount at 1000 m depth (ES 115). The remaining records listed above refer only to post larvae of this species found in samples from greater depths where a massive but non-viable settlement occurs from pelagic larvae probably originating from the upper slope populations (Gage & Tyler, 1981*a*), Semenova, Mileikovsky & Nesis (1964) and Tyler & Gage (1982*b*), show that a form of *'Ophiopluteus ramosus'* which Geiger (1963) and the above authors indicate to be abundant in the surface zooplankton in spring in parts of the N Atlantic, is most probably the pelagic larval stage of this species. We suggest that *O. gracilis* may have a ribbon-like distribution along the upper continental slope, and on submerged banks around the 1000 m depth level, around the N Atlantic.

REMARKS. The evidently high population densities (Semenova *et al.*, 1964; Gage & Tyler, 1981*a*) suggest that *O. gracilis* might be extensively preyed on by bottom feeding fish: remains of this species are identifiable and commonly found in stomachs of demersal fish trawled on the Hebridean slope (Mauchline & Gordon, personal communication).

Close-up bottom photographs taken at around 1000 m on the Hebridean slope only rarely show brittle stars (A. J. Southward, Marine Biological Association, Plymouth, personal communication). Possibly the individuals of this abundant population are shallow burrowers, or lie with the mottled coloured disk closely pressed against the sediment or with a dusting of particles covering it. The markedly long oral and arm tube-feet of this species may be associated with a microphagous feeding mechanism.

Ophiocten hastatum Lyman, 1878

See: Paterson, Tyler & Gage, 1982: 117–119.

SAMPLES. ES 6 (9; ? [juveniles] 4), ES 10 (1; ? [juveniles] 2), ES 27 (1; ? [juvenile] 1), ES 31 (1), ES 52 (2), ES 55 (1), ES 56 (2; ? [juvenile] 1), AT 107A (10), ES 111 (1), AT 119 (1), AT 121 (187), ES 129 (1), ES 137 (4; ? [juvenile] 1), ES 140 (7), ES 143 (? 4), ES 147 (7), ES 152 (2), ES 164 (? 1), ES 185 (5). OTSB 51001 (1). [2000 m to 2921 (? 2925) m]

DISTRIBUTION. This species may now be regarded as cosmopolitan in distribution, with a bathymetric range in the lower abyssal from 1130 to 5000 m, but concentrated on the lower abyssal zone. Paterson, Tyler & Gage (1982) in re-examining species of the genus *Ophiocten* have found no significant differences between *O. hastatum* and *O. latens,* records of the latter being confined to the Atlantic.

Ophiura affinis Lütken, 1858

See: Süssbach & Breckner, 1911 : 244–247; Mortensen, 1927 : 244–245, fig. 132.

SAMPLE. ES 113 (10). [168 m]

DISTRIBUTION. Although not apparently recorded previously on Rockall Bank this record is not unexpected in view of the known distribution in the NE Atlantic and around the British Isles (e.g., Farran, 1913; Mortensen, 1927; D'yakonov, 1954; Ursin, 1960); 8–550 m.

Ophiura carnea Lütken, 1858

See: Mortensen, 1927 : 243, fig. 131.

SAMPLES. ES 2 (1), AT 194 (1). [630–2857 m]

DISTRIBUTION. *Ophiura carnea* is an eastern Atlantic species found from Norway south to the Bay of Biscay, previously collected also from the upper Porcupine Seabight by the *Helga* from 215 m to *c.* 400 m (Farran, 1913); 50–1260 m.

The present records are the first for this species in the Rockall Trough, that from the Anton Dohrn Seamount, AT 194 in 630 m depth, is well within the previously recorded range; the one from ES 2 in 2857 m depth represents a considerable extension to the known bathymetric range.

Ophiura irrorata (Lyman, 1878)

See: Lyman, 1882 : 47, pl. 5, figs 7–9; Mortensen, 1933 : 86–87, fig. 48.

SAMPLES. AT 151 (2), AT 175 (1), AT 177 (1), AT 181 (1), AT 191 (59), AT 192 (220), AT 195 (1), AT 198 (1). [1862–2220 m]

DISTRIBUTION. This is a cosmopolitan abyssal species; Mortensen (1933) gives the known bathymetric range as 600–4315 m.

A few specimens were found in Agassiz hauls at St. 'M'. However, hauls on two positions on the Feni Ridge yielded by far the largest samples indicating a more numerous development of the population there. All specimens agreed with Mortensen's (1933) description of *O. irrorata* sensu stricto. When compared with localities worked on the eastern side of Rockall Trough, the small numbers or apparent absence of this species seems striking. Possibly, *O. irrorata* is associated with conditions, such as strong bottom currents, that are best developed on Feni Ridge.

REMARKS. The colour of fresh specimens is a pale pink with a dark blue-purple colouration where the stomach shows through the dorsal and ventral disk. The tube feet on the arms are a pale orange colour which immediately distinguishes them from the bright red tube feet of *O. ljungmani* when found in the same haul.

Ophiura imprudens (Koehler, 1906)

See: Koehler, 1907 : 256, pl. 18, figs 9–10.

SAMPLE. ES 113 (6). [168 m]

DISTRIBUTION. This species has only been recorded once before, off the Azores; 560 m.

The present record from Rockall Bank of this evidently rare species is somewhat shallower at 168 m.

Ophiura ljungmani (Lyman, 1878)

See: Mortensen, 1927 : 240–242, fig. 130.

SAMPLES. ES 2 (55), ABD 3 (? 7), ES 4 (1464), ES 6 (1439), ES 8 (? 36), ES 10 (juveniles, 6120), ES 12 (548), ES 14 (32), ES 15 (243), ES 20 (juvenile, 1), ES 27 (170), ES 28 (25), ES 31 (25), ES 32 (1) ES 34 (1164), SBC 46 (3), ES 52 (53), ES 53 (15), ES 54 (1), ES 55 (851), ES 56 (688), ES 57 (921), SBC 58 (5), ES 59 (425), SBC 60 (juveniles, 4), SBC 68 (juvenile, 1), ES 69 (juveniles, 2), ES 99 (juveniles, 8), AT 107A (2), ES 111 (205), ES 112 (44), ES 118 (201), AT 119 (2), AT 121 (640), ES 129 (512), ES 135 (973), ES 137 (787), AT 138 (2), AT 139 (8), ES 140 (1056), AT 141 (50), ES 143(107), AT 144 (3), ES 147 (965), SBC 150 (4), AT 151 (8), ES 152 (360), AT 153 (47), AT 154 (12), ES 164 (530), AT 167 (49), ES 169 (323), AT 171 (17), ES 172 (270), AT 175 (15), ES 176 (289), AT 177 (35), ES 180 (291), AT 181 (35), ES 184 (352), ES 185 (74), AT 186 (25), ES 190 (73), AT 191 (65), AT 192 (38), AT 195 (21), ES 197 (5), AT 198 (1), ES 200 (1). SWT 11 (2), SWT 13 (2). [1050 m to 3425–3500 m]

DISTRIBUTION. Commonly occurring throughout the N Atlantic; 309–4070 m (Cherbonnier & Sibuet, 1973).

Ophiura ljungmani was abundant in samples taken at the Permanent Station (2900 m), becoming less numerous at shallower stations where *Ophiomusium lymani* became abundant, although adult specimens were found as shallow as 1632 m on the Hebridean slope. At the latter position, the bottom haul also included adults of *Ophiocten gracilis* occurring near the lower end of the bathyal range of the breeding population. The deepest record of *Ophiura ljungmani* was from 3425–3500 m in the Porcupine Seabight.

REMARKS. The colour of fresh specimens is pale rose to white, with conspicuously bright red tube feet. The stomach shows through the disk as a dark blue-purple colouration.

REPRODUCTION. *Ophiura ljungmani* has separate sexes in roughly equal proportions. Study of the gametogenic cycle shows a marked seasonal periodicity with rapid vitellogenic growth in autumn and maximum development and probable spawnout by late January/early February at the Permanent Station (Tyler & Gage, 1979, 1980). These authors suggest that egg size (max. 90 μm) and fecundity (up to 5700 eggs per individual) indicate planktotrophic larval development.

Analysis of disk-size frequencies from the Permanent Station indicates low survival of the annually recruited postlarvae and a high though constant rate of mortality amongst older year classes. The time series studied at the Permanent Station also suggests both a seasonal growth pattern, with maximal growth in spring, and a variation in year-class strength (Gage & Tyler, 1981*b*). Reproductive maturity is thought to be reached in the third year at a disk diameter of 3·5–4·0 mm with individuals thereafter reproducing annually (Tyler & Gage, 1980).

Ophiura ophiura (Linnaeus, 1758)

See: Süssbach & Breckner, 1911 : 238–241 (as *O. ciliaris*); Mortensen, 1927 : 236–238, fig. 128 (as *O. texturata*).

SAMPLE. ES 23 (1). [704 m]

DISTRIBUTION. Previously recorded all round the coasts in British seas; 0–200 m.

The presence of this well-known coastal species on the upper Hebridean Slope represents a surprising extension of its known bathymetric range.

Subfamily **OPHIOLEPIDINAE**

Ophiomusium lymani Wyville Thomson, 1873

See: Mortensen, 1927 : 253–254, fig. 138.

SAMPLES. ES 4 (153), ES 10 (juveniles, 13), ES 12 (32), ES 14 (10), ES 15 (juveniles, 33), ES 18 (1), ES 20 (juveniles, 4), ABD 24 (1), ES 34 (15), SBC 68 (1), AT 68A (1), AT 107A (192), AT 114 (42), AT 138 (8), AT 139 (14), AT 141 (juveniles, 14), AT 144 (1686), ES 147 (juveniles, 2), AT 151 (233), AT 153 (610), AT 154 (369), AT 157 (3), AT 161 (119), SBC 166 (juvenile, 1), AT 167 (944), AT 169 (juvenile, 1), AT 171 (1565), AT 175 (735), ES 176 (402), AT 177 (1245), AT 181 (1711), ES 182 (140), ES 184 (1174), AT 186 (1027), AT 191 (64), AT 192 (714), AT 195 (1434), ES 197 (308), AT 198 (724), ES 200 (192). SWT 10 (505), SWT 11 (1), SWT 16 (3), SWT 17 (6), SWT 18 (129), SWT 32 (35). [810–2921 m]

DISTRIBUTION. *Ophiomusium lymani* is now known to have a cosmopolitan distribution; 130–3435 m. It was first described by Wyville Thomson (1873) from dredgings by the *Porcupine* in the Rockall Trough. Elsewhere this species has been recorded from between 700 m and 4700 m and at temperatures varying from 2° to 9°C (Cherbonnier & Sibuet, 1973).

Adult specimens in our samples were taken over a wide area and in depths from 810 m on the Hebridean Slope to 2540 m in the central Rockall Trough. Postlarvae of this species are distinctive and easily recognised (see Schoener, 1967); they were common in epibenthic sled hauls taken between these depths and were also found in hauls down to 2921 m depth in the vicinity of the Permanent Station. This suggests that postlarvae dispersed to depths significantly greater than about 2500 m do not survive to adulthood.

REMARKS. The numbers of specimens collected in Agassiz hauls at different depths indicate that the population is best developed around the 2000 m isobath in Rockall. At St. 'M', the population density visible in close-up bottom photographs is a little less than 1 m^{-2} (Dr A. J. Southward, personal communication). Size frequencies from Agassiz hauls at this station show a marked dominance by adults, with a postlarval peak apparent from the fine-meshed epibenthic sled hauls. Although finding no seasonal pattern in oogenesis from comparison of oocyte size frequencies in samples taken at different times of the year, Gage & Tyler (1982) interpret differences in the relative size of the postlarval peak in spring and summer samples as evidence for a seasonal recruitment to the population. A model age structure consisting of two fast growing juvenile year classes with a slowing of growth on attaining reproductive maturity at *c.* 20 mm disk diameter and a consequent 'stacking up' of adult year classes is deduced from study of a time series of disk-size frequencies in large samples of *Ophiomusium lymani* from St. 'M'.

Heavy mortality is thought only to apply to post-larvae; the relatively heavily calcified body and large size of adults protecting them from heavy predation. However, a small percentage (*c.* 2–5%) of specimens show healed, or partially healed, lesions usually in the dorsal interradial area. They may be caused by attacks from biting predators, probably fish. Subsequent regeneration of the wound may give rise to 'monstrous' specimens sometimes found.

Bottom photographs and submersible observations (Barham, Ayer & Boyce, 1967; Wigly & Emery, 1967; Grassle, Sanders, Hessler, Rowe & McLellan, 1975) indicate that this species moves over, or nestles into, the sediment surface without burrowing. Some photographs show the disk raised well clear of the sediment, supported by the proximal part of the arms. Barham *et al.* (1967) suggested that *O. lymani* is a filter feeder; however, the absence of obvious ciliary tracts, long spines and arm podia equipped with mucus producing glands as found in other brittle stars known or likely to filter feed, such as members of the families Amphiuridae, Ophiactidae, Ophiotrichidae and Ophiocomidae (see Fell, 1966 and Reese, 1966 for reviews of pre-1965 literature; Fontaine, 1965; Pentreath, 1970; Warner & Woodley, 1975) seem to render a filter feeding mode of nutrition unlikely for *Ophiomusium lymani.* Preliminary study of the stomachs of specimens from St. 'M' has yielded few recognisable contents, the stomachs of most of 100 specimens examined appearing empty. However, fragments of mysid uropods and small gastropod shells were found along with polychaete setae, indicating that *O. lymani* may rather be an opportunistic scavenger or carnivore.

Discussion

For many relatively well known species that are also abundant in our samples a bathymetric range of adults is recorded that is somewhat narrower than that known over its full range. This is not unexpected considering the comparatively small area of the present study compared to the full geographical range of the deep-sea distribution of a species, when, as seems likely, these distributions are determined chiefly by the temperature of water masses (Ekman, 1953). Examples include the asteroid *Porcellanaster ceruleus* and the ophiuroids *Ophiacantha bidentata, Ophiactis abyssicola, Ophiura ljungmani* and *Ophiomusium lymani.* In addition there are many uncommon species known from great depths to the south that are recorded in the Rockall area at somewhat shallower depth. Examples include the ophiuroids *Ophiotrema alberti, Ophiacantha crassidens* and the asteroids *Pteraster reductus, Hoplaster spinosus.* This may be explained in terms of the general trend towards progressive submergence of the cold, deep ocean water, expressed as a trend to tilting of isotherms in longitudinal sections of the Atlantic Ocean (Wüst, 1936), that is related to the continual formation of deep water from the polar oceans. The species *Ophiacantha cuspidata* provides an illustration of this trend towards an increasingly submerged distribution towards lower latitudes, which is analogous to the bipolar-equatorial submergence seen in distributions of many coastal species in the Atlantic that are described by Ekman, 1953. Mortensen (1927, 1933) cites records made by the *Ingolf* of *O. cuspidata* from SW of Iceland in 1461 m depth, and by the *Challenger* at 785 m depth in the S Atlantic off Ascension Island; while the present records from the Rockall Trough at 55°12´N in 1900 m fall between these depths and the *Princesse Alice* record at 42°53´N in 2460 m off the Azores (Koehler, 1909).

Topographic boundaries such as the Wyville Thomson Ridge give rise to locally sharp step-like increases in the physical gradient where cold arctic water enters the Atlantic deep sea by a process of intermittent overflow (Ellett & Roberts, 1973). The southerly route of this overflow is thought to lie along the sedimentary feature, Feni Ridge, which describes a sinuous path along the eastern margin of the Rockall Bank. The consequent latitudinal difference in hydrographic regime on the west and east sides of Rockall Trough may well be connected with differences seen in the echinoderm fauna around the 2000 m level (Table 1).

Although, as shown in Table 1, more samples have been taken on the east side, a considerably richer echinoderm fauna appears in the few samples taken in the west. Some species recorded there were not taken at all in the east around St. 'M' and the adjacent lower Hebridean slope despite the relatively intense sampling effort made in this area. Many of the species recorded only in the west are uncommon and have, as already discussed, only been previously taken in deeper water to the south. Other more common species, such as *Ophiura irrorata,* appear to be far more numerous on Feni Ridge.

Table 1 Distribution of species on west and east sides of the Rockall Trough. *species present only as juveniles; †probable suspension feeders (see text).

Species taken only from west (on Feni Ridge at 1600–2190 m depth, 5 hauls)	Species common to both areas	Species taken only from east side (on St. 'M' or adjacent Hebridean Slope at 1600–2200 m depth, 23 hauls)
Heliometra glacialis	*Porcellanaster ceruleus*	*Rhizocrinus lofotensis*
		? *Hathrometra sarsi*
**Psilaster andromeda*	*Bathybiaster vexillifer*	*Dytaster insignis*
Evoplosoma scorpio	*Plutonaster bifrons*	*Pectinaster filholi*
**Pteraster reductus*	*Benthopecten simplex*	*Hoplaster spinosus*
†*Asteroschema inornatum*	*Pseudarchaster parelii*	**Paragonaster subtilis*
†*Ophiotrema alberti*	*Hymenaster membranaceus*	†*Asteronyx loveni*
†*Ophiacantha crassidens*	*Ophiacantha bidentata*	*Homalophiura tesselata*
†*O. cuspidata*	†*Ophiactis abyssicola*	
†*O. simulans*	†*Amphilepis ingolfiana*	
Amphiophiura saurura	*Ophiochiton ternispinus*	
? *Stegophiura macrarthra*	*Ophiura ljungmani*	
Ophiocten hastatum	*Ophiura irrorata*	
	Ophiomusium lymani	

It is tempting to account for the presence of these species as essentially abyssal elements that find the cooler water overflowing from the Arctic to their liking. However, hydrographic data given by Ellett & Martin (1973) although showing some east–west tilting of deep-water temperature and salinity isopleths indicates that this explanation may be insufficient: samples from the Permanent Station at 2900 m where the bottom water generally is as cool as in shallower water to the west on Feni Ridge have not yielded the missing species.

It seems more likely that hydrographic conditions other than temperature may also be important in the west. Since overflow is thought to be associated with fast bottom currents and high turbidity (Jones, Ewing, Ewing & Eittreim, 1970), it seems possible that the richer fauna may reflect the better feeding conditions, particularly for microphagous suspension feeding, in the nepheloid layer at the benthic boundary. Hence, it may be significant that six out of the eleven species found as adults only from the Feni Ridge are likely, on morphological criteria, to be suspension feeders (Table 1). However, one difficulty with this explanation is that the apparently higher species richness of echinoderm groups covered by the present account on Feni Ridge is also associated with physical conditions that, because of the episodic nature of overflow, are more variable than elsewhere. Although admittedly we are dealing with only a fraction of the total benthic fauna, the present data do not accord with the stability-time hypothesis invoked by Sanders (1968, 1969) to explain why species richness in the supposedly stable environment of the deep sea appears to be higher than in comparable coastal habitats where conditions for life are more variable. It is interesting to note that results from two other studies of deep-sea faunas (Rex, 1973; 1976; Thistle, in press) do not fit in with the prediction of a simple positive relationship between increasing physical stability and species richness. Furthermore, the results of intensive sampling in the Bay of Biscay indicate that species diversity of asteroids on the lower continental slope decreases with increasing depth after a maximum at 2200 m (Sibuet, 1977), despite a presumed increasing physical stability with increasing depth. Rex (1981) has re-analysed data available from the NW Atlantic to show a parabolic response of species diversity of both macrofauna and megafauna to depth, with maxima at levels from 1900 m to 2800 m.

The present study also demonstrates a greater geographic and bathymetric range of juveniles and post-larvae of some relatively abundant species compared to the adult range. Juveniles of the following species of sea star have been identified over a wider bathymetric range than adults: *Plutonaster bifrons, Pectinaster filholi, Pseudarchaster parelii* and *Hymenaster membranaceus.* Juveniles and post-larvae of brittle stars usually are smaller than those of sea stars. However, Gage & Tyler (1981*a*) have shown that a massive non-viable settlement of the upper bathyal brittle star *Ophiocten gracilis* occurs seasonally over a wide area of the Rockall Trough. The easily recognisable post-larvae and juveniles of *Ophiomusium lymani* also are found in samples from a wider range of depths than adults. Post-larvae are typically found in small numbers in epibenthic sled hauls from the Permanent Station (*c.* 2900 m) at a depth several hundred metres deeper than the lower limit of adults. We suggest that the probably demersal lecithotrophic larvae are dispersed by currents to areas sometimes inimical to adult survival. Post-larvae of other ophiuroid species have also been identified in the Permanent Station samples; one of these being an ophiacanthid, probably *Ophiacantha bidentata,* that probably is derived from an adult population in shallower water, since no adult ophiacanthid species has as yet been collected from the Permanent Station.

Summary

Four species of sea lily, forty species of sea star and thirty-six species of brittle star are identified from recent extensive sampling conducted by the Scottish Marine Biololgical Association from R.R.S. *Challenger* in the deep sea area lying to the west of the British Isles. The following species have not previously been recorded from the British seas.

Crinoidea	*Thaumatocrinus jungerseni*
Asteroidea	*Hyphalaster inermis* *Pseudarchaster gracilis* *Paragonaster subtilis* *Pteraster* sp. aff. *P. acicula* *Hymenaster gennaeus* (provisionally) *H. rex* *Freyella spinosa* *F. sexradiata* *Hydrasterias sexradiata*
Ophiuroidea	*Astrodia tenuispina* *Asteroschema inornatum* *Ophiotrema alberti* *Ophiomyces grandis* *Ophiacantha cuspidata* *O. simulans* *O. aculeata* *Ophiolimna bairdi* *Amphiura otteri* *A. griegi* *Amphilepis ingolfiana* *Homalophiura tesselata* *Amphiophiura convexa* *A. saurura* ? *Stegophiura macrarthra* *Ophiocten hastatum* [Hoyle (1884) records this species but under the name *O. sericeum*] *Ophiura irrorata* *O. imprudens*

Ophiura imprudens is known from only one specimen from the Azores and *Ophiacantha aculeata* only from N America and SW Iceland.

Extensions of bathymetric range are recorded (in metres) for the following:

	Upper limit	Lower limit
Crinoidea		
Thaumatocrinus jungerseni		2734–3425 (3500)
Heliometra glacialis		1358–1900
Asteroidea		
Luidia ciliaris		400–650 (805)
Plutonaster bifrons		2500–2965
Psilaster andromeda		1853–2965
? Radiaster tizardi		1320 (? 1630)–2540
Paragonaster subtilis	2455–(1785) 1845	
Plinthaster dentatus		2117–2190
Evoplosoma scorpio		*c.* 1600–1900
Pteraster reductus	1920–1900	
Hymenaster gennaeus		2245–2500 (2500)
H. rex		2285–2910
Henricia abyssicola	*c.* 930–168	
Brisinga endecacnemos		2200–2220
Freyella spinosa		4060–4810
Stichastrella rosea		1150 (? 1330)–1632
Zoroaster fulgens		3660–4810
Ophiuroidea		
Astrodia tenuispina		3300–3425 (3500)
Asteroschema inornatum		1480–1900
Ophiotrema alberti	3785–1862	
Ophiacantha aculeata		2510–3425 (3500)
Ophiolimna bairdi		2600–2910
Amphiura otteri		1425–2892
A. griegi		300–810
Amphipholis squamata		740–1330
Amphiophiura convexa	2160–1997	
? *Stegophiura macrarthra*		424–1900
Ophiura carnea		1260–2857
O. imprudens	560–168	
O. ophiura (syn. *O. texturata*)		200–704

In this list the depths given are the minimum possible extensions of the previously known bathymetric limits. Figures in brackets give the maximum possible from the depth range of hauls (fish trawlings only) although of course specimens may not have been taken throughout the depth range of the tow.

For some of the more abundantly occurring species from fine-meshed epibenthic sled hauls, the records demonstrate a wider bathymetric distribution of juveniles and post-larvae than of adults, suggesting that externally developing larvae often are dispersed to areas where they do not survive to adulthood.

In general, records of adults of the most abundantly occurring species cluster well within the vertical range recorded over their, often circumoceanic, known distribution. This may reflect a trend towards progressive submergence of isotherms in the deep ocean from high to low latitudes.

Despite a concentration of sampling effort to the east, comparison between the east and west sides of Rockall Trough has indicated that a richer echinoderm fauna, particularly of filter feeding species, is present in the west on Feni Ridge. This may be related to a greater availability of suspended food in the west associated with the passage of fast-flowing turbid water at the benthic boundary as a result of overflow from the Faroe Channel over the Wyville Thomson Ridge.

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British Museum (Natural History)
The Red Notebook of Charles Darwin

Edited by Professor Sandra Herbert

Charles Darwin used the pocket-sized Red Notebook to record various observations and ideas over the course of the year from mid-1836 to mid-1837. It was an important year, spanning the last months of the voyage of H.M.S. *Beagle* and the first months back in England. The notebook contains observations on points visited, reading notes, and speculations on theoretical questions. The theoretical questions Darwin considered in the notebook pertain primarily to geology, where he was interested in finding an explanation for the rise and fall of the earth's crust, and to the subject of the mutability of species. Most significantly, the Red Notebook contains the earliest known evidence of Darwin's adoption of an evolutionary hypothesis. The notebook also reveals Darwin's dependence on professional zoologists working in London for technical judgements decisive for his adoption of an evolutionary position.

Sandra Herbert is Associate Professor in History at the University of Maryland Baltimore County and is the author of several studies of various aspects of the early career of Charles Darwin.

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Miscellanea

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The cranial muscles of loricarioid catfishes, their homologies and value a taxonomic characters (Teleostei: Siluroidei). By G. J. Howes

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The cranial muscles of loricarioid catfishes their homologies and value as taxonomic characters (Teleostei: Siluroidei)

Gordon J. Howes

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The cranial muscles of loricarioid catfishes, their homologies and value as taxonomic characters (Teleostei: Siluroidei)

LIBRARY

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Introduction

The Loricariidae are a family of Neotropical siluroids (catfishes) with two outstanding external features: an 'armoured' body and a sucker-like ventrally situated mouth. The bodies of the catfishes are virtually encased in a series of bony plates or scutes reflecting the muscle segmentation (see Alexander, 1965: 136) and the heads are covered with a mosaic of bony plates. The bony plates generally run in an overlapping series of 5 longitudinal rows, but in those forms with an attenuated and compressed caudal peduncle, the series may be reduced posteriorly to two. All the plates, most of the head covering, the fin spines and rays bear spines. In some taxa, particularly in males, the spines may form dense clumps on the tops and lateral parts of the head. The operculum and interoperculum also bear spines which on the latter, may be attenuated and hooked.

The spines, or denticles all appear to have a similar structure, namely dentine surrounding a pulp cavity and with an enamel cap (see Bhatti, 1938). Thus, to all intents and purposes they are to be regarded as teeth. Ørvig (1977) used the term 'teeth' for those dental elements confined to the jaws and 'odontodes' for similar elements occurring on the extra-oral dermal skeleton. In this paper, 'odontodes' will be used to refer to such spines, prickles and bristles on the scutes, head and fin rays.

The sucker-like mouth is in the form of reflected upper and lower, usually papillate, lips. They surround highly mobile jaws (see p. 343) which often bear long, usually bifid, hooked teeth. The jaws may be long and shallow with the teeth numerous, arranged in regular rows e.g. *Chaetostoma,* short and deep with the teeth few and clumped together e.g. *Pseudacanthicus,* or lamellate and edentulous, some *Loricaria.*

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Alexander (1965) has described the mouth and its functional morphology. He showed how the modified mouth, body scutes and fins are all features associated with the torrential and benthic environments of loricariids.

In terms of numbers of taxa, the Loricariidae is the largest siluroid family, containing *ca* 70 genera and 600 nominal species (Isbrücker, 1980). Whether or not this number of taxa are a reflection of the taxonomic concepts of various authors is a matter for debate (see. p. 339) but even if many proved to be synonyms, it is likely that the family would retain its numerical supremacy.

Of the currently recognized genera (Isbrücker, 1980) approximately 50% occur in the Amazon basin, 30% in Guianas, 20% in both the Orinoco and trans-Andean regions, 25% in Parana, 15–16% in the Magdalena and Andes, and 10% in south-eastern Brazil.

The biology of loricariids is poorly known. Most appear to feed on algae or perhaps organisms that live in algal mats. Angelescu & Gneri (1943) found that different taxa fed on molluscs, chironomid larvae, mud and diatoms. Many species live amongst stones and roots and some *Hypostomus* live in tunnels in muddy river banks (Vaz-Ferreira & Senorans, 1971).

The development of long odontodes on the head and anterior borders of the pectoral fin spines are sexually dimorphic characters in some taxa, *Ancistrus, Loricaria* and *Lithoxus*; their function is discussed later, p. 343.

There exists no comprehensive work on loricariid anatomy. Regan (1904; 1911) listed a series of osteological characters by which he defined the family and its subunits. Leege (1922), Peyer (1922), Starks (1926), Gregory (1933), Angelescu & Gneri (1943), Chardon (1968), Alexander (1964; 1965) and Lundberg & Baskin (1969) are the principal sources of information on various osteological features. Of these papers, only those of Alexander, Chardon and Lundberg & Baskin have provided anything approaching a comparative analysis of the family with other siluroids. Even so, the number of taxa whose anatomy has been described has been exceedingly small.

Only one paper, that of Alexander (1965), has described the musculature of loricariid fishes in any detail. The earlier paper by Leege (1922) has negligible myological information. Alexander limited his description of jaw musculature to *Hypostomus,* = *Plecostomus* in Alexander, and the opercular musculature (part) of *Ancistrus.* Alexander's work was aimed primarily at a functional description, and detailed myological description was lacking.

The principal aim of this paper is to go some way towards filling the lacunae of knowledge about loricariid myology. By making out-group comparisons with other siluroids and otophysans the muscular system of loricariids are viewed in terms of character states and used to construct a cladogram. This scheme is compared with others utilizing selected osteological characters and the resultant information is used to produce a cladogram of nested synapomorphies for those taxa studied. No detailed treatment of loricariid interrelationships is presented. As yet no cladistic framework is available for any group of siluroid fishes and so any comments on interrelationships must be regarded as highly speculative.

Some attention is given to the possible function of the muscular systems described.

Muscle nomenclature

The *adductor mandibulae* muscle complex of teleostean fishes is usually recognised as being divisible into several elements each identified by a lettering sequence A_1–A_w, following Vetter (1878). As various subdivisions of these elements have been recognised, they have been identified by addition of a subscript letter or numeral. This system of nomenclature has, in some instances, resulted in complex notations (see for example Matthes', 1963, system for cyprinids). More important, however, is whether those elements similarly labelled in different taxa represent homologues—a question discussed later (p. 323).

In most siluroids, the morphology of the *adductor mandibulae* is complex, and this is particularly so in loricariids. In order to clarify the following descriptions the muscles are shown schematically in Fig. 1.

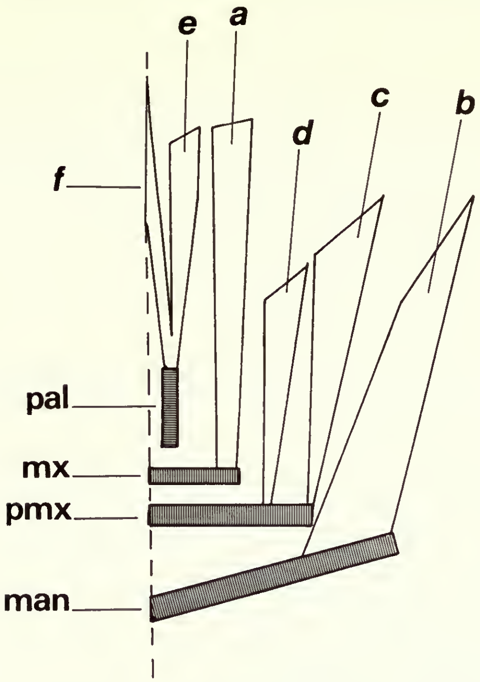


Fig. 1 Schematic diagram of loricariid jaw-palatine muscles and their insertions.

The outer part of the adductor muscle complex, which in more advanced teleosts runs to the maxillary bone of the upper jaw, designated as A_1, inserts, in siluroids, on to the lower jaw. The muscle having its insertion on to the maxilla is recognised as the *retractor tentaculi.* The phylogenetic origin of this muscle is possibly from a medial part of the *adductor mandibulae;* see Howes (1983), and below, p. 327 for discussion of homology. The number of medial divisions of the adductor complex in loricariids exceeds that of other siluroids, and possibly that of other otophysans. This multiplication of elements leads to difficulties in using the generally applied system of notation since their respective homologies are uncertain (see p. 327). Thus, for descriptive purposes all jaw muscles are designated **a-f**.

Muscle **a** is that inserting on the maxilla; muscles **b-d** are various divisions of the *adductor mandibulae;* muscles **e-f** attach to the palatine bone and are derivatives of the *adductor arcus palatini.*

Other suspensorial, opercular and hyoid muscles are named according to the nomenclature of Winterbottom (1974) and their homologies with those muscles so named in other teleosts are accepted.

Specimens examined

The specimens listed are those dissected for this study. In addition, dissections, skeletons, alizarins and radiographs of specimens representing nearly all siluroid families have been examined.

Loricariidae: *Ancistrus occidentalis* 1981.1.5:722–748; 749–797
Ancistrus stigmaticus 1901.5.8:10 (skeleton)
Ancistrus spp Uncatalogued (skeleton)
Chaetostoma anomalum 1903.6.30:102 (skeleton)
Chaetostoma breve 1898.11.4:38 (skeleton)
Chaetostoma dermorhynchus 1880.12.8:64–66
Chaetostoma microps 1981.1.5:821–867

Cochliodon cochliodon 1981.1.5:777–787
Cochliodon sp. Uncatalogued (alizarins)
Farlowella knerii 1880.12.5:206 (skeleton)
Farlowella spp Uncatalogued (inc. alizarins)
Hemiancistrus megacephalus 1972.10.17:872–875
Hemiodonichthys acipenserinus 1879.12.1:75–79; 1977.3.10:186
Hemipsilichthys calmoni 1929.2.1:66–71
Hypoptopoma carinata 1926.10.27.367–73
Hypostomus plecostomus 1981.1.5:760–776
Hypostomus spinossisimus 1898.11.4:30–31
Hypostomus verraes 1895.3.29:38 (skeleton)
Ixinandria montebelloi 1981.11.30:13–15
Lipopterichthys carrioni 1935.5.20:18–27
Lithoxus lithoides 1972.7.17:66–115
Loricaria cataphracta 1926.3.2: 765–82; 1860.11.10:15 (skeleton)
Loricaria brunneus 1981.6.9:1074–1081
Loricaria jubata 1914.5.18:68–72
Loricaria labialis 1934.8.20:368–388
Loricaria lanceolata 1981.1.5:873–904
Loricaria microlepidogaster 1929.2.1:29–50
Loricaria platystoma 1974.5.22:544–545
Loricaria simillima 1934.8.20:326–46
Loricaria strigilata 1929.2.1:31–40
Loricaria teffeana 1895.5.17:103 (skeleton)
Loricaria variegata 1914.5.18:73
Loricaria venezeuelae 1947.7.1:228–232
Loricaria spp Uncatalogued (alizarins)
Metaloricaria nysseni 1982.4.7:7
Rhadniloricaria macromystax 1869.5.21:8
Neoplecostomus granulosus 1896.7.4:3–5; 6 (skeleton)
Otocinclus nigricauda 1934.8.20:220–240 (alizarin)
Panaque nigrolineatus 1974.8.14:13–15
Peckoltia pulcher 1980.7.1:87; uncatalogued
Pogonopoma wertheimeri 1904.1.28:6
Pogonopomoides parahybae 1904.1.28:7
Pseudacanthicus serratus 1870.3.10:4 (skeleton)
Pseudancistrus barbatus 1972.7.17:49–50
Pseudohemiodon sp. Uncatalogued
Pseudohemiodon laticeps 1895.5.17:113–4
Pterygoplichthys anisitsi 1934.8.20:255–64
Pterygoplichthys multiradiatus 1897.12.1:280 (skeleton)
Stoniella leopardus 1973.7.17:188–198
Sturisoma panamense Uncatalogued
Sturisoma lyra 1897.12.1:72 (skeleton)

Astroblepidae: *Astroblepus festae* 1894.11.4:18 (skeleton)
Astroblepus heterodon 1910.7.11:138 (skeleton)
Astroblepus grixalvii 1898.11.4:12–17
Astroblepus cf. *praeliorum* 1969.1.27:35–46

Callichthyidae: *Callichthys callichthys* 1981.6.9:995–1005; uncatalogued
Hoplosternum littorale 1934.9.12:413–420

Diplomystidae: *Diplomystes papillosus* 1889.11.14:33; 1896.10.2:22 (skeleton)

Doradidae: *Amblydoras hancocki* 1971.4.14:15–30

Mochokidae: *Euchilichthys royauxi* 1909.4.29:98–102

Nematogenyidae: *Nematogenys inermis* 1883.11.27:45–48; 49 (skeleton)

Scoloplacidae: *Scoloplax dicra* UMMZ 198967, Paratypes (inc. alizarins)

Sisoridae: *Glyptosternum cous* 1968.12.13:471–76
Glyptothorax major 1978.3.20:286–289

Trichomycteridae: *Branchioica magdalenae* 1947.7.1:203–8 (alizarins)
Eremophilus mutisii 1978.2.22:16
Trichomycterus cordovense 1911.11.25:1–10
Trichomycterus rivulatus 1944.6.16:142–5

Description of loricariid cranial muscles

Jaw muscles

Whilst the jaw muscles of loricariid fishes differ in their arrangement from those in other siluroids (see p. 323), within the group there is a high degree of uniformity. Differences are marked by the relative size of each muscle and by varying points of insertion. Both variables are diagnostic for sub-groupings within the family.

In order to present a succinct comparative analysis, the jaw musculature of one taxon will be described in detail and attention drawn to taxa which differ from that plan. The representative taxon is *Pterygoplichthys anisitsi.* Choice of this species is determined by its representing the largest group of loricariids—the subfamily Hypostominae (see p. 338), and by what may be termed its relatively generalised morphology. This latter impression does not imply that the taxon is primitive or plesiomorphic.

When the thick, plate-like epidermis is removed from the side of the head in *Pterygoplichthys* three large muscles are exposed. The medial, band-like muscle (**a**, Fig. 2A) originates from the lateral margin and ventral surface of the lateral ethmoid passes laterally to the palatine and inserts on the maxilla. The maxillary ramus of the trigeminal nerve runs along its lateral border and sends a branch into the muscle's ventral surface. The buccal ramus passes across the dorsal surfaces of the muscle and the palatine to enter the maxilla.

The outer muscle (**b**), originates below the eye and inserts on the lower jaw. Its lateral fibres originate from the fascia of the cheek armour, the posterior fibres from the preoperculum, and the medial fibres from the hyomandibula and pterygoid. There is a continuity of origin across all the bony medial elements and it is not possible to differentiate individual muscle segments. The lower jaw insertion is somewhat complex (Fig. 2B). Prior to insertion the outer bloc of fibres bifurcates, one bundle inserting on the medial margin of the dentary, the other on the coronoid process. Both insertions are musculose. An inner slip of fibres, arising from the pterygoid is also differentiable from the anterior part of the main muscle mass. This muscle slip turns medially around the anterior border of the pterygoid to insert tendinously on the inner aspect of the dentary.

Lying medial to muscle **b** is a long, almost cylindrical muscle, **c**, which originates from the hyomandibula; its anterior part passes medially below muscle **a** and inserts tendinously onto the premaxilla.

Medial to muscle **c**, and extending along the pterygoid, is a thin, narrowly triangular muscle (**d**, Figs 2B & 3A). Its origin is from the hyomandibula and its insertion is into a complexly divided connective tissue sheet. This sheet has attachments to the ventral surface of the palatine, to the upper surface of the premaxilla, and to the dentary (Fig. 3A).

In *Pterygoplichthys* there is a tendinous insertion on the premaxilla, although the dorsal part of the muscle is firmly attached to the palatine. The mandibular trunk of the trigeminal nerve passes across the face of muscle **c**, to make a slight loop below it and attach to its ventral border by connective tissue. From this point the nerve curves downward into muscle **b** and passes between the bifurcation of that muscle into the dentary-anguloarticular foramen to innervate the outer tissues of the lower jaw.

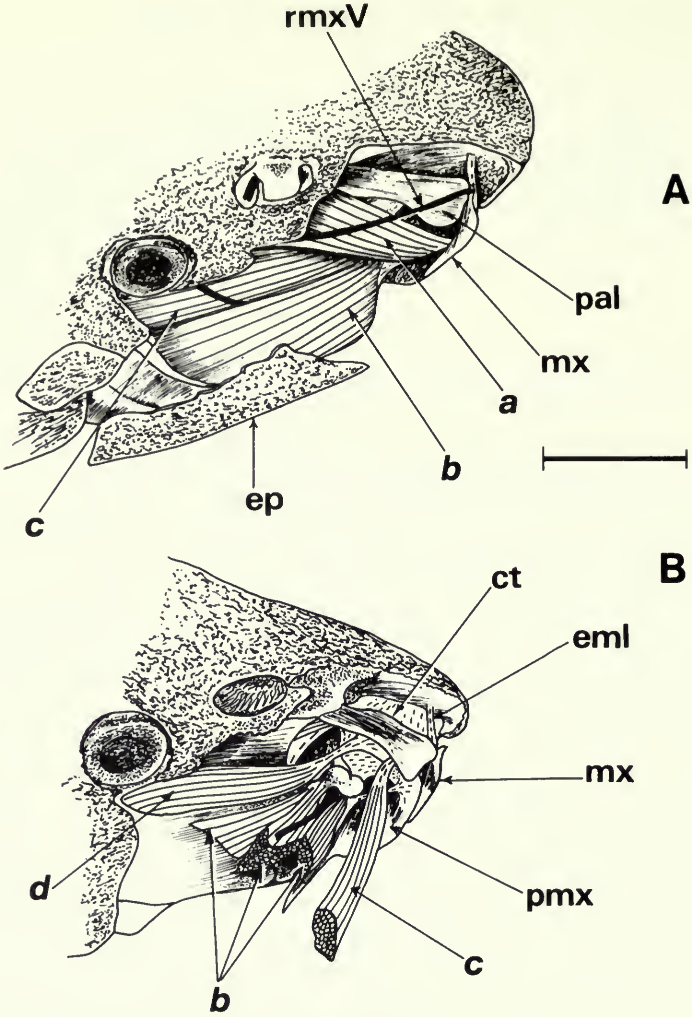


Fig. 2 Jaw muscles of *Pterygoplichthys anisitsi* (BMNH 1234.8.20: 255–64). A, superficial musculature, dorsal view; B, deeper muscles with muscle **a** removed, dorso-lateral view. Scale = 10 mm. eml = ethmo-maxillary ligament: ep = epidermis; pal = palatine.

Muscles **e** and **f** (Fig. 3B) operate the palatine; muscle **e** originates from the medial face of the pterygoid and from the ventral surface of the lateral ethmoid, its insertion is onto the postero-ventral margin of the palatine. The fibres deriving from the pterygoid are horizontally aligned whereas those stemming from the lateral ethmoid are aligned at angles varying between 20°–45° to the horizontal. Muscle **f** originates from the ventro-medial surface of the lateral ethmoid and from the ventral surface of the frontal. It inserts on the posteromedial aspect of the palatine. A strong ligament connects the posterior lateral face of the palatine with the anterior border of the pterygoid.

In *Pterygoplichthys* muscle **e** lies in a pterygoid channel. The lateral wall of the channel rises to meet the lateral ethmoid margin and so totally encloses the muscle which exits through an anterior vertical slit. Alexander (1965) described a similar feature in *Hypostomus*.

Variants to the jaw muscle pattern described above occur in a group of taxa represented by *Hemipsilichthys* and *Chaetostoma* where muscle **a** is broadened and fan-like so that it completely covers muscle **c** (Fig. 4A). In species of this group the suspensorium is orientated into an almost horizontal plane, so that muscle **b** bulges laterally.

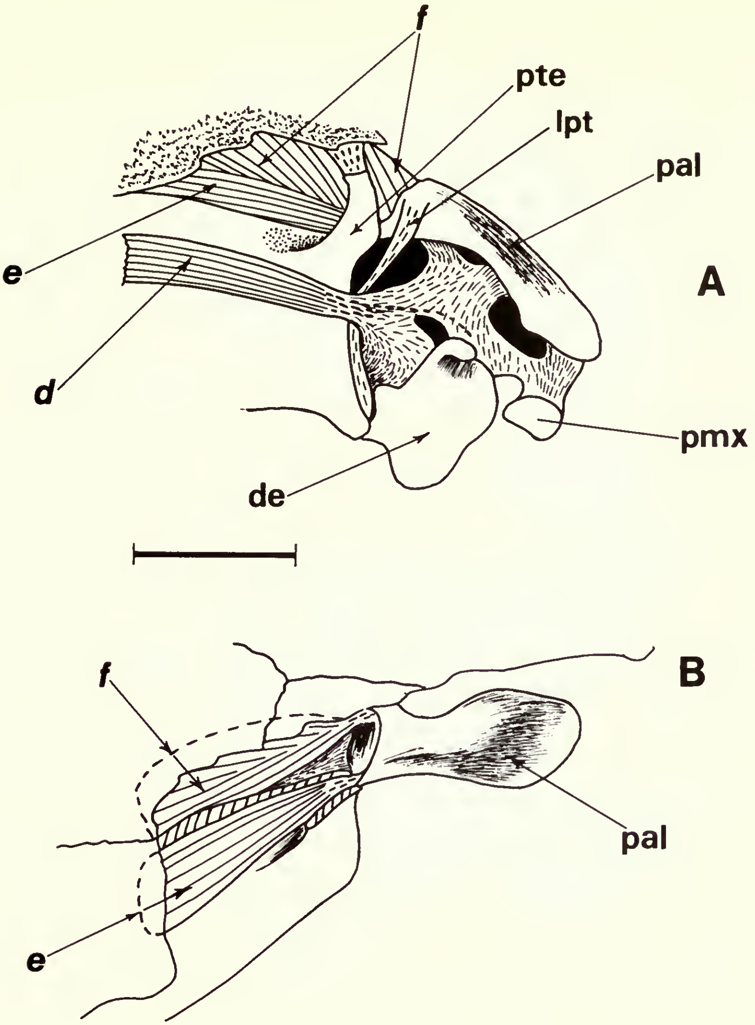


Fig. 3 *Pterygoplichthys anisitsi,* A, insertion of inner jaw muscle **d**, lateral view; B, configuration of *extensor tentaculi* muscle in dorsal view. The cut surfaces of the pterygoid are shown hatched. Scale = 3 mm. lpt = pterygoid-palatine ligament.

More marked differences occur in a group containing *Loricaria, Sturisoma* and *Farlowella* (Figs 5A; 6). Used here, *Loricaria* corresponds to the broad concept of Regan (1904) rather than the restricted one of Isbrücker (1981); see further discussion on p. 338. In these genera muscle **c** inserts on the premaxilla *via* a thick tendon whose length is correlated with that of the snout. The tendon passes through a loop of connective tissue at the rostro-ventral margin of the palatine, to turn through a right angle before its premaxillary insertion (Fig. 6, **tc**). Muscle **d** is directed medially, its tendon of insertion running into the palatine-premaxillary connective tissue and almost meeting its antimere in the midline before joining the premaxilla. In *Sturisoma,* the muscle is attached to the ventro-posterior part of the palatine as in *Pterygoplichthys.*

In some *Loricaria* species there are distinct dorsal and ventral portions of muscle **a**. The lower portion (**av**, Fig. 5A) inserts on the wide, convex dorsal surface of the palatine, its postero-medial fibres are inseparable from those of muscle **e**; the upper part (**ad**) runs forward to insert on the maxilla as in other loricariid taxa.

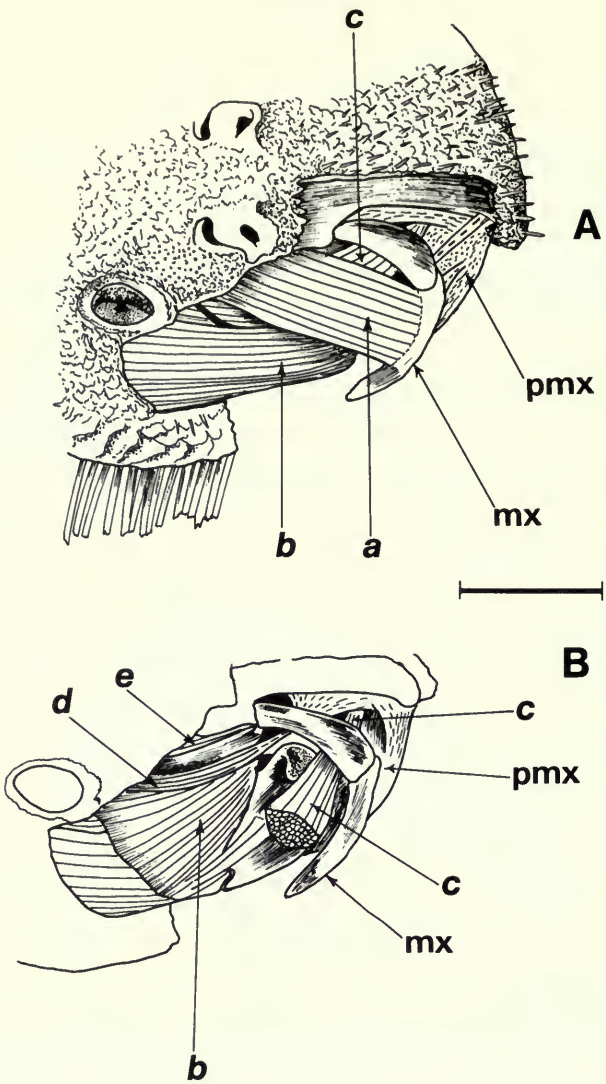


Fig. 4 *Hemipsilichthys calmoni* (BMNH 1929.2.1: 66–71). A, superficial musculature; B, deeper muscles with muscle **a** removed; both in dorsal view. Scale = 10 mm.

Farlowella differs from *Loricaria* and *Sturisoma* in that muscle **a** is enclosed within a pterygoid channel similar to that in *Pterygoplichthys*. *Pseudohemiodon* and *Hemiodonichthys* depart in several respects from the above arrangements (Fig. 5B). Muscle **a** is a narrow, strap-like element; muscle **c** does not insert directly on the maxilla but runs into an extensive tissue sheet connecting the pterygoid, palatine, premaxilla and maxilla; muscle **d** inserts, *via* a long tendon, on the premaxilla and maxilla; muscle **e** inserts tendinously onto the ventral centre of the lamellate palatine.

Two other genera which depart from the generalized jaw muscle plan are *Hypoptopoma* and *Otocinclus* (Fig. 7). In these genera, muscle **a** occurs as the most lateral of the superficial jaw muscles. It runs from the laterally shifted lateral ethmoid (see p. 332) to insert tendinously into the centre of the maxilla. Muscles **b** and **c** have their 'normal' insertions onto the lower jaw and premaxilla respectively. Muscle **d** joins a thick connective tissue band linking the palatine and premaxilla.

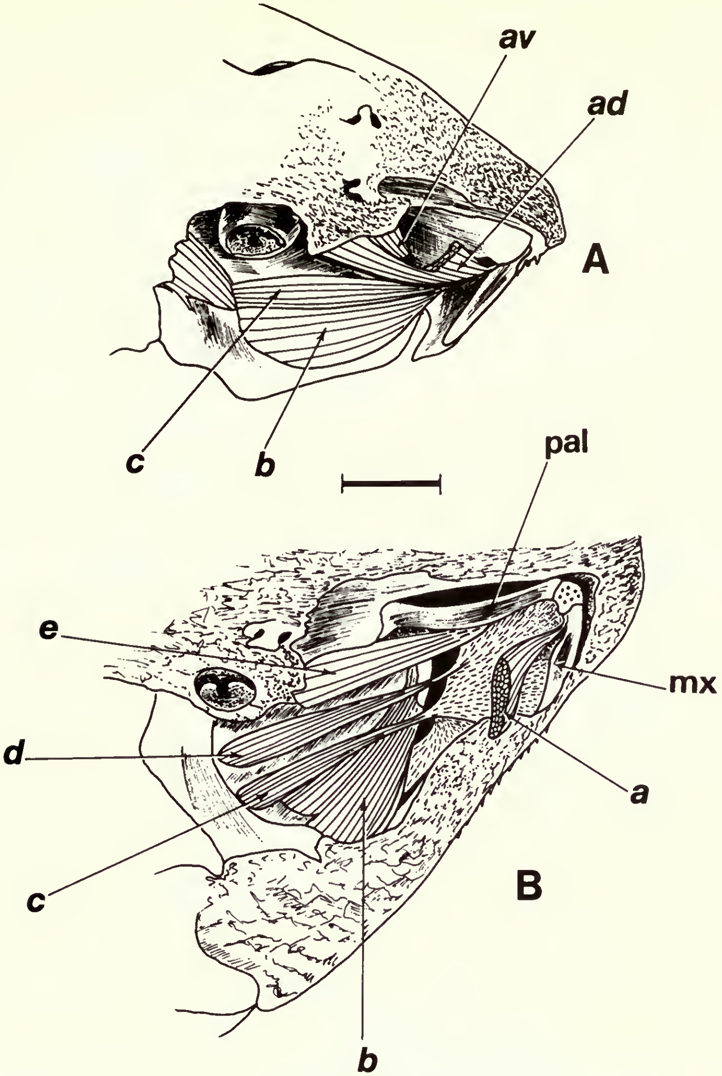
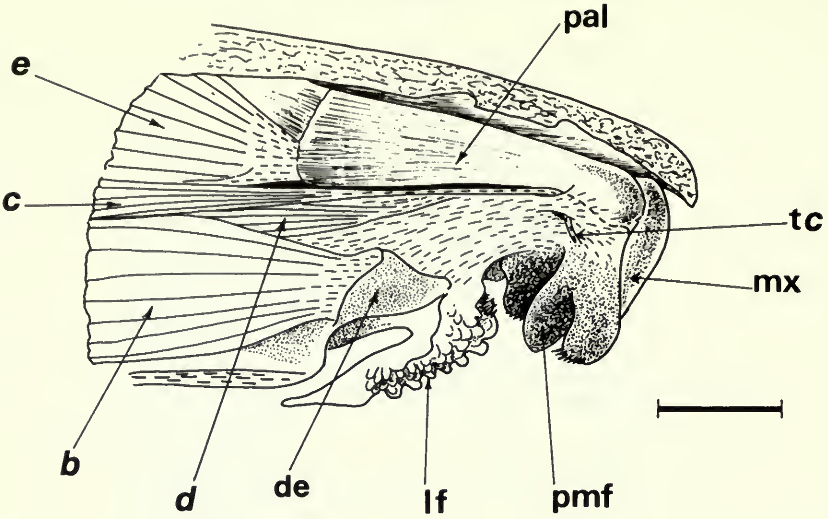


Fig. 5 Jaw and palatine muscles of A, *Loricaria strigilata* (BMNH 1929.2.1: 31–40) in dorso-lateral view; B, *Pseudohemiodon* sp. (uncatalogued) in dorsal view. Scale = 5 mm.

Hyoid muscles

The muscles serving the lower jaw, and having their origins from the hyoid bar, have a uniform morphology in the Loricariidae.

The *intermandibularis* is relatively feeble compared with that in other siluroids. It is most highly developed in *Pterygoplichthys* (Fig. 8A) where its lateral insertion is bifurcate, the inner part joining the dentary, the outer attaching to the loose connective tissue at the rictus of the mouth. In other loricariid taxa the *intermandibularis* is a thin band of muscle fibres which in broad-mouthed genera, e.g. *Chaetostoma, Pseudancistrus, Lipopterichthys,* attaches laterally to the reflected lip tissue (Fig. 8B).


pal
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c
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pmf

Fig. 6 *Metaloricaria nysseni* (BMNH 1982.4.7:7) showing insertions of deeper muscles; lateral view. lf= lower labial tissue; pmf=premaxillary medial labial fold; tc=insertion tendon of muscle c. Scale=5 mm.

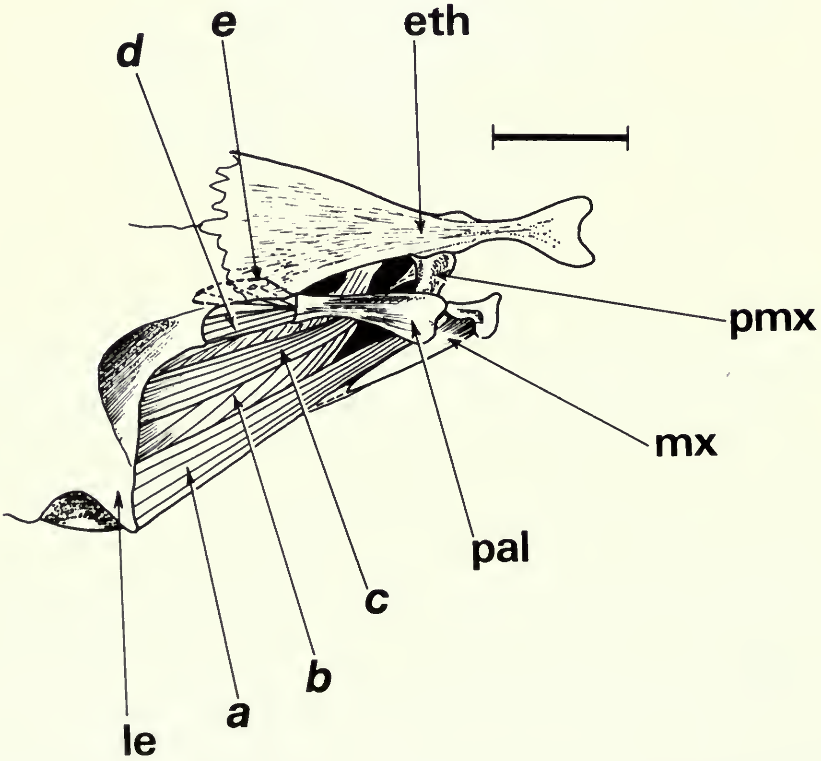
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Fig. 7 *Hypoptopoma carinatum* (BMNH 1973.3.27: 3) jaw muscles in dorsal view. Scale= 1 mm.

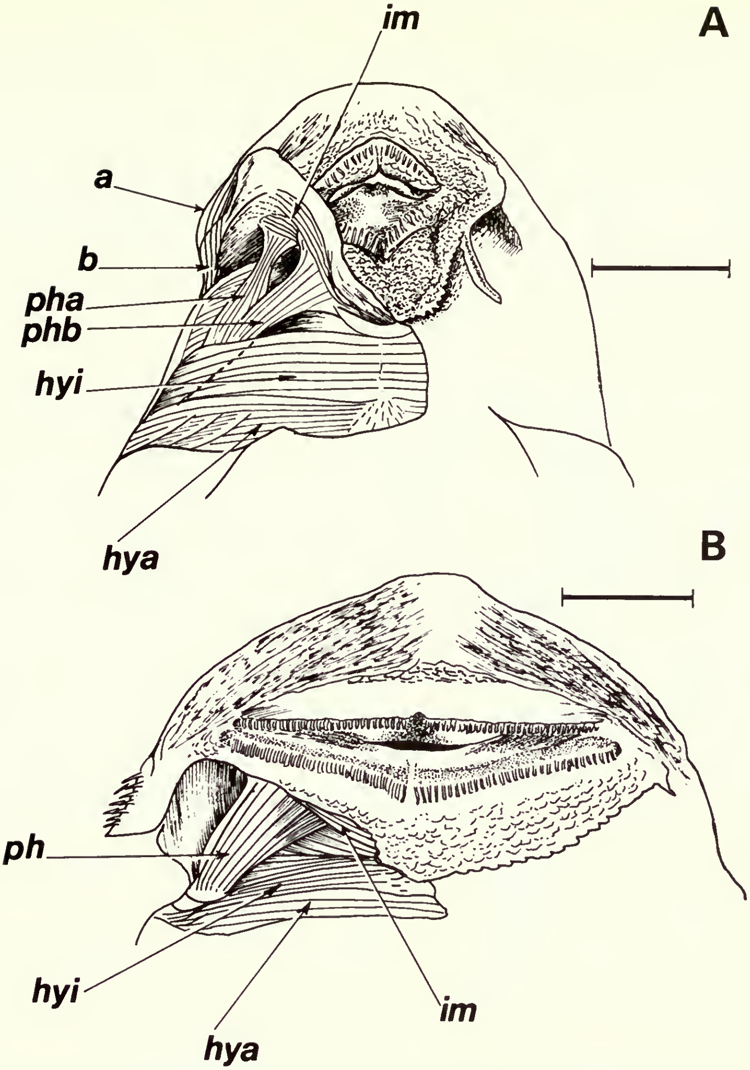

Fig. 8 Hyoid muscles of A, *Pterygoplichthys anisitsi* (BMNH 1934.8.20: 255–64); B, *Chaetostoma acquinoctialis* (BMNH 1978.7.14: 20), both in ventral views. Scales = 5 mm. **ph, a, b** = divisions of *protractor hyoidei*; **hya, hyi** = *hyohyoideus adductores* and *inferioris;* **im** = *intermandibularis.*

The *protractor hyoideus* is well-developed and extends between the posterohyal and anterohyal to the lower jaw (Fig. 8A). The fibres from the left and right hyoid bars do not meet in the midline as in other siluroids and indeed, in most teleosts. Each part of the muscle is divided for almost its entire length into two segments (**Pha, Phb,** Fig. 8A). One lies dorsomedially and attaches to the dentary, the other is ventro-lateral and attaches to the dorsal face of the reflected lip tissue.

The largest hyoid muscle in loricariids is the *hyohyoides inferioris* which extends laterally from the midline of the urohyal to the anterohyal and posterohyal. In *Cochliodon, Panaque* and *Hypostomus,* the lateral border of the muscle has a marked concave indentation to allow for the bypass of the *protractor hyoideus.* The *hyohyoidei adductores* extend from the upper medial face of the operculum, between the branchiostegal rays, to a midline raphe above the *sternohyoideus.*

Opercular and suspensorial muscles

The muscles having the greatest degree of variability in size and position are those controlling the opercular apparatus.

In *Pterygoplichthys* the *dilatator operculi* muscle is a thin, narrow element running along a hyomandibular groove. It originates from a pterotic fossa and inserts on the antero-medial border of the operculum (**do** Fig. 9A). The *levator operculi* muscle originates from the pterotic-posttemporal = temporal plate of Regan, 1904, and inserts on the dorso-medial margin of the operculum (**lo**, Fig. 9A). The *adductor operculi* originates from a cavity formed

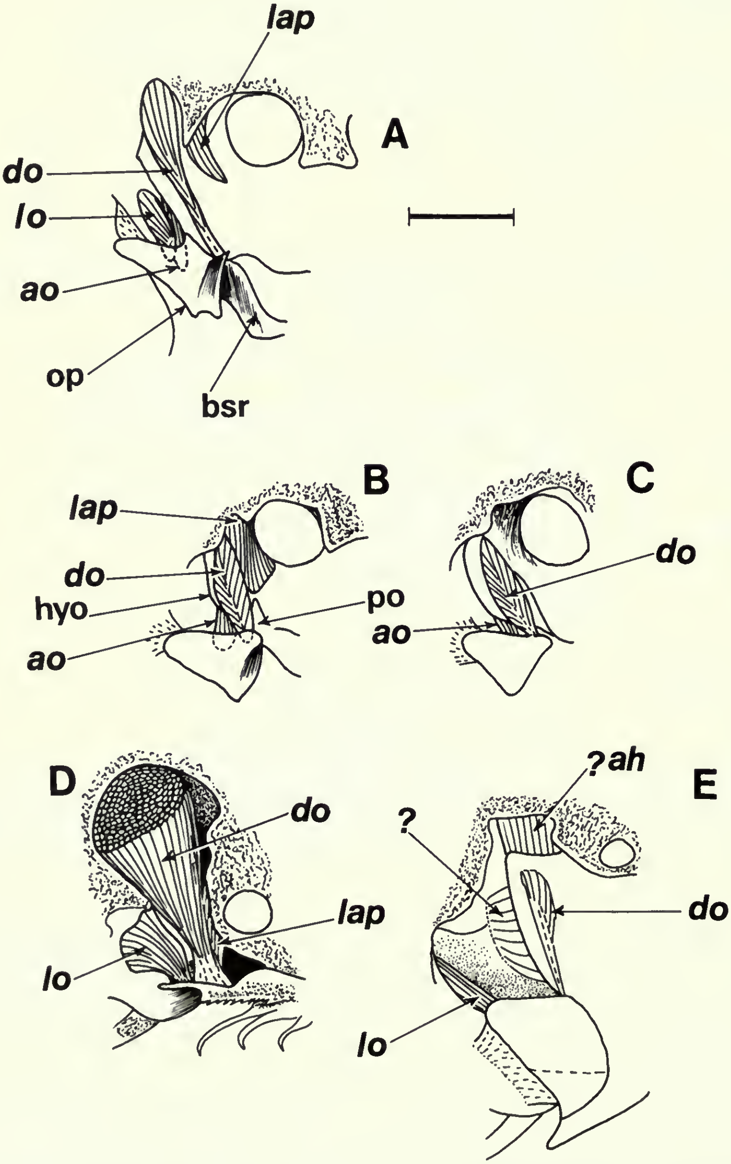

Fig. 9 Opercular and suspensorial muscles of A, *Pterygoplichthys anisitsi;* B, *Loricaria simillima;* C, *Loricaria cataphracta;* D, *Ancistrus occidentalis*; E, *Pseudohemiodon* sp. Scale = 5 mm. A–D in dorso-lateral, E in dorsal views. **ah** = *adductor hyomandibularis;* po = preoperculum; bsr = branchiostegal ray.

between the hyomandibula and pterotic, to run almost vertically behind the hyomandibula and insert on the central dorso-medial aspect of the operculum (**ao**, Fig. 9A).

In *Pterygoplichthys* the *levator arcus palatini* is a thin, vertically aligned muscle extending between the sphenotic and hyomandibula (**lap**, Fig. 9A). The *adductor arcus palatini* muscle in all loricariids examined runs laterally and almost horizontally from the posterior part of the parasphenoid to the medial face of the hyomandibula. It is probably more correct to refer to this muscle as the *adductor hyomandibulae* (see Winterbottom, 1974: 239) as it is a separate element from the anterior part of the *adductor arcus palatini* which is modified, as in most siluroids, to form the *extensor tentacularis* muscles (see p. 328).

Apart from minor variations in the orientation of the muscles, the above descriptions of opercular and suspensorial muscles in *Pterygoplichthys* are applicable to *Hypostomus* and *Hemiancistrus.*

In *Neoplecostomus,* the *dilatator operculi* inserts on the dorsal rather than the anterior aspect of the opercular margin. The interoperculum in *Neoplecostomus* is also larger than that in other loricariid genera.

Pseudacanthicus, Pseudancistrus, Stoniella, Cochliodon and *Panaque* show a departure from the hypostomine opercular muscle pattern. The *dilatator operculi* is shifted more anteriorly so as to run across the posteromedial aspect of the orbit. The muscle passes, laterally, beneath a bridge formed by the preoperculum and pterotic-posttemporal plate before inserting on the reduced operculum. In *Panaque* the *dilatator operculi* is situated so far anteriorly that it crosses the medial centre of the orbit (Fig. 10). In these five taxa the *levator operculi* originates from a ventral cavity in the pterotic-posttemporal plate and inserts *via* a thin tendon along the thickened dorso-medial edge of the operculum. The *adductor operculi* appears to be represented by a small slip of muscle running horizontally from the pterotic-posttemporal to insert on the posterior border of the preoperculum, thus running along the top of the bridge beneath which the *dilatator operculi* emerges. There is no connection of the *adductor operculi* with the operculum. In *Pseudacanthicus, Stoniella* and *Panaque* there are evertible 'interopercular' spines (see p. 334).

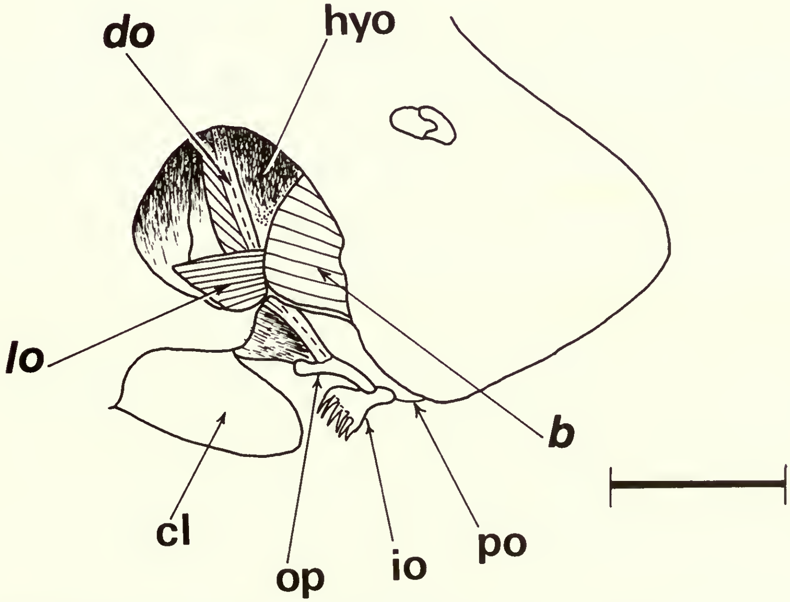

Fig. 10 Opercular muscles of *Panaque nigrolineatus* (BMNH 1974.8.4: 13–15), in lateral view. Scale = 10 mm. cl = cleithrum; io = interoperculum; hyo = hyomandibula; po = preoperculum.

In *Hemipsilichthys* and *Chaetostoma* the *dilatator operculi* is thin and tendinous. It originates from the pterotic and runs outward at an angle of 30° to the horizontal in a lateral hyomandibular groove. The *adductor* and *levator operculi* muscles are of similar morphology to those in *Pterygoplichthys*. The *levator arcus palatini* is, however, smaller, occupying a postorbital space between the sphenotic and hyomandibula.

In *Ancistrus* the opercular muscles are hypertrophied. The *dilatator operculi* muscle is extensive, originating from the roof of the cranium and the supraoccipital (Fig. 9D). The central tendon runs antero-laterally at an angle of about 45°c to the vertical and attaches to the postero-dorsal aspect of the operculum. The operculum is modified to form a mechanism for rotating the 'interoperculum' laterally; described below (p. 334).

The *levator* and *adductor operculi* muscles are well developed, the *adductor* originating from a ventral process of the fused vertebral complex and directed ventro-laterally at 35° to the vertical. The *levator arcus palatini,* instead of inserting on the suspensorium, as in other loricariids, joins the insertion tendon of the *dilatator operculi* and thus appears to reinforce the adduction of the operculum.

In *Loricaria* and *Sturisoma,* the *dilatator operculi* originates principally from the hyomandibula, a few antero-ventral fibres take their origin from the posterior rim of the preoperculum. In some species of *Loricaria,* e.g. *L. simillima,* the muscle's origin is shared in part with that of the *levator arcus palatini* which is also well developed (Fig. 9B). In other species, e.g. *L. cataphracta,* the *levator arcus palatini* is absent (Fig. 9C).

In all *Loricaria* species examined the *levator operuli* is absent; the *adductor operculi* originates from a pterotic-posttemporal cavity. In *Sturisoma* a few tendinous fibres passing along the dorso-medial surface of the operculum may represent the *levator operculi,* and the *adductor operculi* may be represented by a few fibres emanating from the anterior fascia of the body musculature, which at this point is directed laterally to insert on the pterotic-posttemporal plate.

Farlowella possesses a similar morphology of the *dilatator operculi* and *levator arcus palatini* muscles to that of *Loricaria.* In this genus both *adductor* and *levator operculi* muscles are present but weakly developed.

In *Pseudohemiodon* and *Hemiodonichthys* the *dilatator operculi* is reduced virtually to a tendon which runs in a lateral hyomandibular groove. Insertion is on to the antero-dorsal corner of the operculum. *Levator* and *adductor operculi* muscles are absent. Instead, the medial wall of the operculum provides the site of attachment for lateral fibres of the *hyohyoideus adductores* muscle (9E). There is no *levator arcus palatini* muscle in these taxa.

Hypoptopoma and *Otocinclus* both have a feeble *dilatator operculi* originating from the hyomandibula and inserting on the antero-dorsal point of the operculum. A *levator operculi* is present but weakly developed and runs forward ventro-laterally from a medial fascia of the epaxial musculature.

The *levator arcus palatini* originates from a sphenotic fossa, runs outward at an angle of 45° to the vertical and inserts on the hyomandibula just anterior to the ventral part of the *dilatator operculi.*

Summary of muscle systems

From the data presented above, the following groups of loricariid catfishes are discernible on the basis of correlated myological features:

1. *Jaw muscles:* muscle **a** narrow, band-like, lying straight and lateral to the mesethmoid, inserting on the maxilla; muscle **b** inserting entirely on the lower jaw; muscle **c** inserting on the premaxilla; muscle **d** inserting on the premaxilla *via* a connective tissue sheet which attaches to the dentary and the palatine; muscle **e** running through a well-developed pterygoid channel to insert on the palatine. *Opercular muscles:* usually well-developed; *levator arcus palatini* (LAP) small. *Hyoid muscles: intermandibularis* well-developed, sometimes bifurcated laterally, *hyohyoidei inferioris* with concave lateral border, *protractor hyoideus*

with bifurcate insertion to the lower jaw, *hyohyoidei adductores* attaching to the medial face of the operculum.
Included genera: *Neoplecostomus, Hypostomus, Pterygoplichthys, Hemiancistrus.*

2. *Jaw* and *hyoid muscles* as (1). *Opercular muscles: dilatator operculi* shifted anteriorly medial to orbit; *adductor operculi* bridges pterotic-posttemporal plate and preoperculum.
Included genera: *Panaque, Cochliodon.*

3. *Jaw and hyoid muscles* as (1), but no pterygoid channel accommodating muscle **e**. *Opercular muscles* as (2).
Included genera: *Stoniella, Pseudacanthicus, Pseudancistrus, Acanthicus.*
4. *Jaw* and *hyoid muscles* as (1), but muscle **a** expanded concomitantly with increased maxillary length; muscle **e** running in pterygoid channel. *Opercular muscles: dilatator operculi* mostly tendinous and obliquely angled laterally. LAP considerably reduced.
Included genera: *Hemipsilichthys, Lipopterichthys, Chaetostoma, Lasiancistrus.*
5. *Jaw* and *hyoid muscles* as (1). *Opercular muscles* hypertrophied, *dilatator operculi* originating from supraoccipital, *levator operculi* from the complex vertebrae.
Included genera: *Ancistrus, Lithoxus.*
6. *Jaw* and *hyoid muscles* as (1), but muscle **d** directed medially, its tendon of insertion almost meeting its antimere; muscle **a** in some *Loricaria* partly inserting on palatine; muscle **e** in *Farlowella* and *Loricaria platystoma* enclosed in a pterygoid tunnel. *Opercular muscles: dilatator operculi* variably developed; *levator* and *adductor operculi* muscles always reduced, sometimes absent. LAP absent in some *Loricaria* species.
Included genera: *Loricaria, Farlowella, Sturisoma.*
7. *Jaw* and *hyoid muscles* as in (1), but muscle **d** with long insertion tendon; muscle **e** inserting into the centre of the palatine ventrally. *Opercular muscles* reduced, *levator* and *adductor operculi* absent. LAP absent.
Included genera: *Pseudohemiodon, Hemiodonichthys, Crossoloricaria.*
8. Jaw muscles differ from all the above in that muscle **a** lies laterally to the other adductor musculature, otherwise as in (1). *Opercular muscles* reduced.
Included genera: *Hypoptopoma, Otocinclus.*

Out-group comparisons and homologies of loricarioid jaw muscles

A broad comparison of siluroid jaw muscles is presented elsewhere (Howes, 1983) and analysis is here restricted to the following taxa:
Diplomystes, the single genus comprising the family Diplomystidae, considered by most authors to be the most 'primitive' extant siluroid.
Nematogenys, the single genus comprising the family Nematogenyidae. Recent authors, Gosline (1945), Chardon (1968), Arratia *et al.* (1978) include this genus within the Trichomycteridae. For reasons given here (p. 329), I follow Eigenmann (1928) in recognising the genus as representing a distinct family.
Astroblepus, the single genus comprising the family Astroblepidae. Regan (1911) and Gosline (1947) both considered the astroblepids a subfamily of the Loricariidae. I follow Eigenmann (1910) in regarding them as a distinct family (see p. 341). Differences in dentition and cranial osteology suggest that there are possibly two genera contained within *Astroblepus.*

Representatives of the Trichomycteridae and Callichthyidae, both families believed by Chardon (1968) to be related to loricarioids. The terms 'loricarioid' refers to the members of the Loricariidae plus the Astroblepidae, and 'loricariid' to members of Loricariidae only.

In the majority of siluroids the *adductor mandibulae* inserts on the lower jaw. Plesiomorphically, as in *Diplomystes* and *Nematogenys,* divisions of the muscle block are absent or poorly differentiated. The outer, most massive part of the muscle originates from the preoperculum, hyomandibula and usually the quadrate, and inserts onto the outer face of the anguloarticular-dentary. This arrangement has been found in all siluroids examined and it was the contention of Fink & Fink (1981) that a lower jaw insertion of the outer part of the muscle (A_1) was an apomorph character of siluroids (but see below, p. 327).

Although in loricariids a major portion of the *adductor mandibulae,* termed muscle **b** in this text, does insert on the lower jaw, medial portions, muscles **c** and **d,** pass *via* thin tendons running through the palatal connective tissue to the premaxilla (see Fig. 3A).

As stated by Alexander (1965: 135), in the Callichthyidae the superficial part of the *adductor mandibulae,* which he believed to be a combined $A_1 + A_2$, inserts partly on the lower jaw and partly on the anguloarticular-maxillary ligament, whilst a medial part inserts on the outer face of the lower jaw. The situation is rather more complex than that outlined by Alexander since the dorsal part of the adductor can be distinguished as a separate element. Thus, the adductor morphology in callichthyids may be described as follows: An element originating from the hyomandibula, just postero-ventral to the orbit, inserts tendinously on the antero-medial process of the maxilla (**rt**, Fig. 11). The larger part of the adductor originates posteriorly from the preoperculum, medially from the hyomandibula and laterally from the 3rd infraorbital. Its antero-ventral fibres insert on the medial and dorsal aspects of the anguloarticular, the dorsal fibres share the points of insertion on the maxilla with those of the more dorsal muscle, ?A_1 (Fig. 11B). As noted above, the deeper part of the muscle inserts entirely on the lateral face and dorsal margin of the anguloarticular.

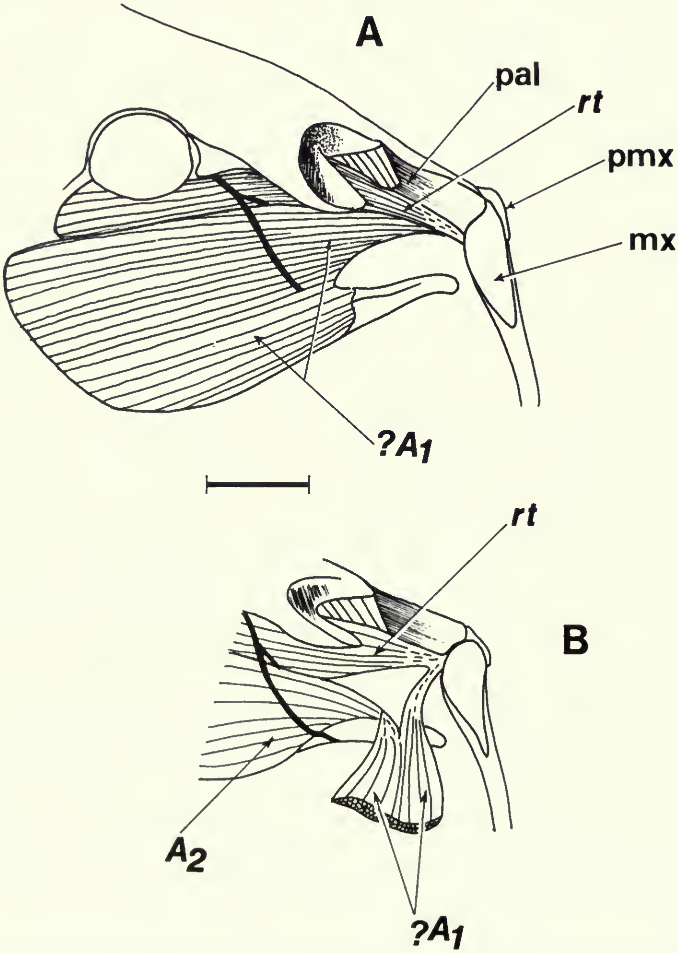

Fig. 11 Jaw muscles of *Hoplosternum littorale* (BMNH 19434.9.12: 413–420). A, superficial musculature; B, deep muscles; both in lateral view, Scale = 5mm. **rt** = *retractor tentaculi.*

As in loricariids, the superficial part of the principal muscle is separated from its medial portion by the ramus mandibularis nerve trunk. In this respect, the outer portion, which has its insertion on the upper and lower jaws, should be considered as A_1; whilst the medial part having its insertion entirely on the lower jaw should be considered as A_2. The dorsal muscle, which has its insertion on the maxilla, is equivalent to the *retractor tentaculi* in loricariids and other siluroids, except that its origin is posterior rather than anterior to the orbit. That this muscle appears to be a dorso-medial part of the adductor, lends credence to the idea that phylogenetically, the *retractor tentaculi* originated from a medial part of the adductor muscle complex (see Alexander, 1965; Howes, 1983).

In *Diplomystes* and *Nematogenys* the *adductor mandibulae* is relatively undifferentiated, the outer part of the muscle running on to the lateral aspect of the anguloarticular, its dorsal fibres inserting *via* a thick tendon on to the dorsal rim of the dentary. The tendon is continuous with a thick 'ligamentous' tissue attaching to the maxilla (see Howes, 1983).

In the Trichomycteridae, the *adductor mandibulae* is also relatively simple (Fig. 12A).

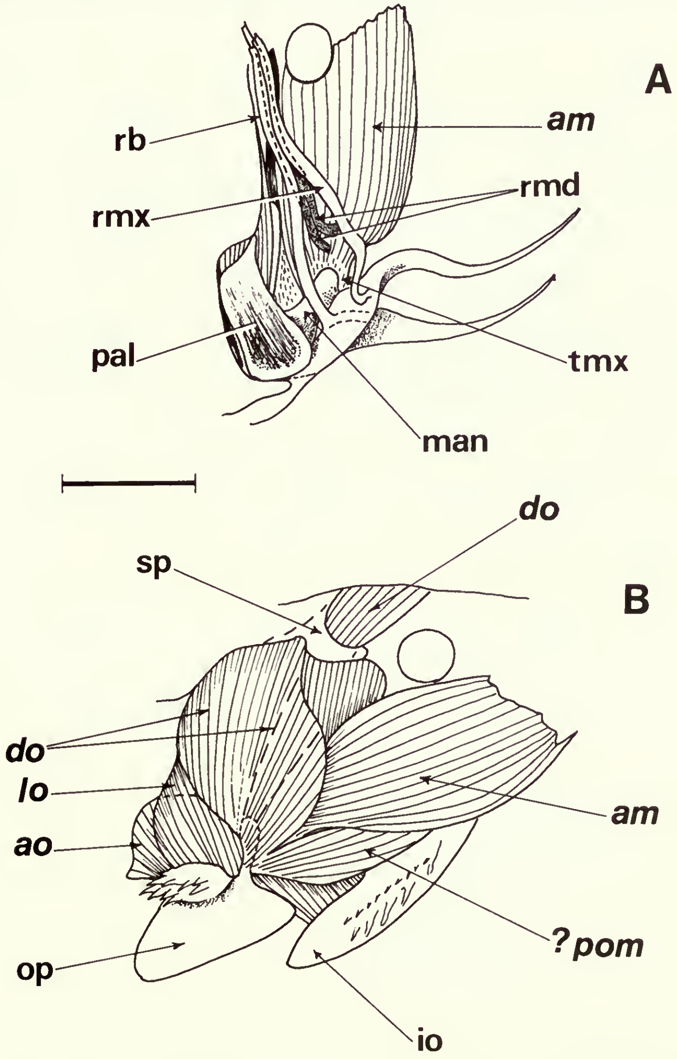

Fig. 12 *Trichomycterus rivulatus* (BMNH 1944.6.16: 142–45). A, superficial jaw muscles in dorsal view. B, posterior jaw and opercular muscles, la lateral view. Scale = 5 mm. **am** = *adductor mandibulae*; **pom** = preopercular muscle; man = mandible; rb = buccal ramus of facial nerve; rmd = mandibularis nerve; sp = sphenotic; tmx = tendon of adductor muscle to maxilla.

The outer portion inserts on the lower jaw but a tendon runs forward into connective tissue attaching to the maxilla. A medial section of the muscle, ?A_2, inserts into the inner aspects of the dentary.

In the Astroblepidae, the *adductor mandibulae,* muscle **b**, is as in the Loricariidae, with the outer portion being divided from the inner by the mandibularis nerve (Figs 13A & B). The outer portion inserts on the rim of the anguloarticular, whilst the inner inserts on the medial face of the dentary. Muscle **c** is also present but is deeper and thicker in the Loricariidae. Two portions of this muscle are discernible, a broad dorsal segment and a deep medial one. The ventral fibres of the medial segment originate from the inner part of the muscle **b**, the remainder from the ptergyoid. The dorsal fibres of the upper portion originate from the lateral ethmoid and the ptyergoid. Medially the two portions are inseparable but insert on short, separate tendons which join prior to their insertion on the premaxilla (Fig. 13B).

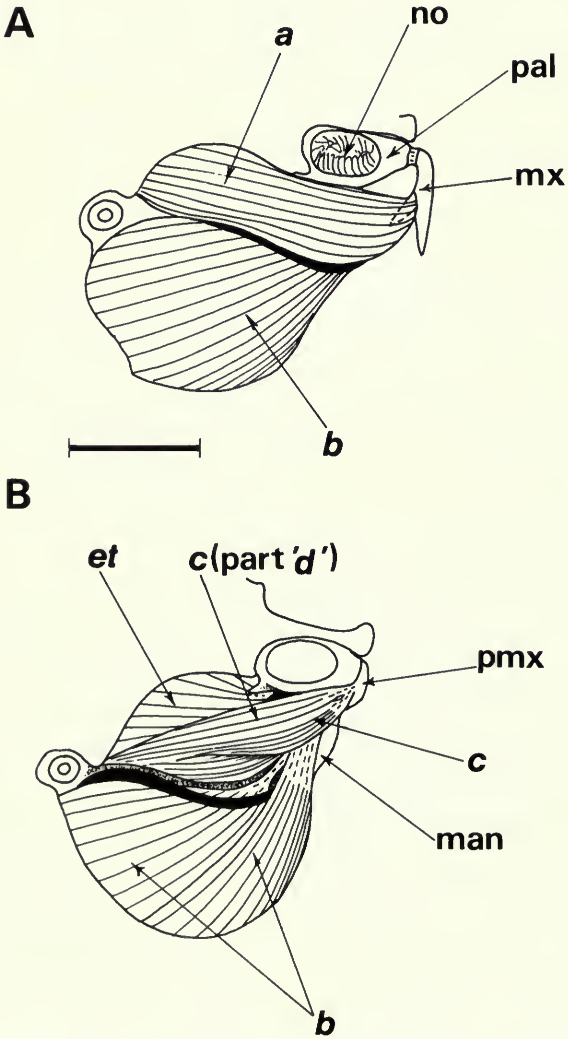

Fig. 13 *Astroblepus cf. praeliorum* (BMNH 1969.1.27: 35–46). A, superficial jaw musculature; B, deep muscles, both in dorsal view. Scale = 5 mm. man-mandible; no = nasal organ.

The morphology of the *adductor mandibulae* in other siluroids is discussed elsewhere (Howes, 1983), but it is pertinent to note here that in none is there a direct connection between the upper jaw and the outer muscle element. It is also argued (Howes, 1983) that this condition is plesiomorphic for otophysans, and that encroachment of lateral fibres to the upper jaw is a derived feature.

The premaxillary insertion of part of the *adductor mandibulae* in the Loricariidae and Astroblepidae, and its maxillary insertion in the Callichthyidae, are viewed as apomorph features. In all three groups, the articulation between the premaxilla and the mesethmoid is a mobile one, a condition not encountered elsewhere in siluroids. In other siluroids, including *Diplomystes,* the premaxilla is firmly united to the lateral extensions of the mesethmoid. Alexander (1965: 134) showed that in *Corydoras* the mouth is protrusile, and this protusibility is partly the result of having a movable premaxilla. It seems likely that because of its restricted distribution amongst siluroids, a movable ethmoid-premaxillary joint is more likely to be a derived character, particularly if *Diplomystes* is viewed as the most plesiomorph extant siluroid (see Fink & Fink, 1981). Suffice it to say that in other otophysans, mobile premaxillary-ethmoid articulations are regarded as derived characters (see Vari, 1979: 272 concerning characoids).

If the plesiomorph conditions of *adductor mandibulae* A_1 in teleosts is regarded as that in which the muscle is inserted on the lower jaw and lies lateral to the mandibular nerve trunk, then muscle **b** in loricariids and astroblepids must be the homologue of A_1. This pattern is, however, further complicated in these two groups by the mandibular nerve trunk entering the muscle mass and passing between two bundles of fibres before entering the lower jaw (see p. 313). Thus, on the strict definition given above, those fibres lying medial to the nerve trunk must be regarded as A_2. This suggestion is supported by the insertion of the medial fibres of muscle **b** on to the coronoid process and medial face of the dentary—which is the usual place of insertion for A_2. Whether the inner slip which in loricariids inserts on the medial face of the dentary should be regarded as A_3 is doubtful, as by definition, A_3 inserts on the anguloarticular. However, it must be borne in mind that the loricariid lower jaw has rotated outward so that the inner surface has come to lie in a horizontal plane with the dentigerous surface forming the anterior border. It may be that coordinate with this rotation, the 'A_3' slip has moved forward from the anguloarticular to the dentary. Thus, it may be concluded that muscle **b** in loricarioids comprises the two elements identified in other otophysans as A_1 and A_2 with the possibility that an inner segment present only in Loricariidae represents A_3.

Muscle **c** lies dorso-medially to the A_1, A_2, A_3 complex and at its hyomandibular origin cannot be separated from the outer combined element. Insertion is *via* a tendon running through connective tissue to the premaxilla. This muscle appears to be the unlabelled dorsal element shown in Alexander's (1965; fig. 17) figure of *Hypostomus.* This element has probably derived from a dorso-medial separation of the *adductor mandibulae.* In *Astroblepus,* the lower portion of muscle **c** is not entirely separated from the outer adductor complex (see above, p. 326 & Fig. 13). This condition suggests that muscle **c** is a derivative of the medial part of the adductor series which has become attached to the premaxilla *via* the connective tissue sheet that connects the lower and upper jaws, and the palatine.

Alexander (1965) applied the name *retractor premaxillae* to the element designated here as muscle **d.** However, it would seem that Alexander overlooked the fact that part of the *adductor mandibulae,* here named muscle **c,** also joins the upper jaw. Concerning functional roles, it would appear that muscle **c** performs the action which Alexander ascribed to muscle **d,** namely being the antagonist of the *extensor tentaculi* muscles, **e** and **f,** and thus retracting the upper jaw. For this reason I am applying the name *retractor premaxillae* to the dorso-medial element designated in this text as muscle **c**.

Muscle **d** which Alexander (1965) recognised as the '*retractor premaxillae*', appears to perform a different function in that, whilst it ultimately inserts into the premaxilla, it is also connected with the lower jaw and with the palatine. In this respect its functional role is not at all clear, but manipulation of preserved specimens indicates that a significant downward movement of the palatine occurs when the muscle is pulled posteriorly. Thus, I will refer to it as the *retractor palatini.* Again, this muscle seems to be a *de novo* development from the inner part of the *adductor mandibulae* complex.

In the Diplomystidae, Nematogenyidae and Trichomycteridae, there is no separate medial muscle attaching to the upper jaw. Only in the Astroblepidae are there elements recognisable as homologues of muscles **c** and **d** in the Loricariidae (p. 326). In most loricariids (e.g. *Pterygoplichthys,* Fig. 3A) muscle **d** (*retractor palatini*) has a plesiomorphic attachment to the underside of the palatine prior to its insertion on the upper jaw. It is hypothesised that phylogenetically the inner part of the *adductor mandibulae* has, in loricariids, shifted from the lower to the upper jaw *via* a connection with the palatine.

Muscle **a** is regarded as the homologue of the *retractor tentaculi* in other siluroids. Along the lateral border of the muscle runs the ramus maxillaris of the trigeminal nerve which bifurcates anteriorly, one branch innervating the dorsal, and the other the ventral fibres of the muscle. The dorsal face of the muscle is crossed by the buccal ramus which terminates in the maxillary tissue. Similar innervations and nerve course are to be found associated with the *retractor tentaculi* of other siluroids (see for example Mithel, 1964). The origin of the *retractor tentaculi* has been the subject of debate (see Winterbottom, 1974), some authors believing the muscle to be derived from A_1 and others that it is a *de novo* development from the medial aspect of the adductor. A more detailed discussion of the matter (Howes, 1983) concludes that the latter is a more likely hypothesis to account for its derivation. The course of the trigeminal nerve rami in *Nematogenys* and the trichomycterids, taxa lacking a *retractor tentaculi,* reinforces this view. Both the buccal and maxillary rami lie medial to the principal muscle mass (Fig. 12A). The only way it is possible for the nerves in loricariids to have come to occupy their present position would have been for a muscle segment to have developed ventro-medially to them and for the nerves to have shifted laterally in relation to the muscle.

The most extreme shift of the *retractor tentaculi* is that in *Hypoptopoma* and *Otocinclus* where the lateral ethmoid has extended so far laterally that the muscle makes an angle of about 45° to the midline.

Muscles **e** and **f** are homologous with the *extensor tentaculi* of other siluroids. Both sections are derivatives of the *adductor arcus palatini* and form the antagonists of the *retractor tentaculi* (see Winterbottom, 1974: 240). In *Astroblepus,* the *extensor tentaculi* is of a primitive, single element whose fibres run laterally from the lateral ethmoid and insert on the posterior portion of the palatine (Fig. 13B). The muscle is floored by a thick tendinous sheet connecting the parasphenoid with the lateral ethmoid processes.

Opercular muscle morphology in loricariids is correlated with the size and position of the opercular bones. In the majority of taxa the operculum is small, with its dorso-posterior border sealed to the pectoral girdle by a membrane, leaving only a ventral opening. Such immobility of the operculum has, in some taxa, led to atrophy or disappearance of the *levator* and *adductor operculi* muscles (see above, p. 322). Although the *dilatator operculi* is sometimes, as in *Pseudohemiodon,* markedly reduced, it is always present and in *Ancistrus* it extends from the dorsal midline of the cranium and cranial roofing bones. In some taxa the *dilatator operculi* originates from the hyomandibula rather than the cranium. The hyomandibula is firmly and immovably articulated with the cranium, dorsally *via* an interdigitation with the prootic, and posteriorly with the pterotic-posttemporal plate; the loss of hyomandibular cranial fossae is synapomorphic for loricariid taxa. The sites of origin of the *levator* and *adductor operculi* muscles are similar to those in other siluroids, although somewhat modified owing to the ventral extension of the pterotic-posttemporal plate. What appears to be the *adductor operculi* in one group of loricardiids (e.g. *Panaque, Pseudacanthicus;* p. 321) has shifted its point of insertion from the operculum to the preoperculum.

The opercular muscles in *Astroblepus* (Astroblepidae) have a relatively plesiomorphic arrangement. The *dilatator operculi* is strongly developed and runs postero-ventrally from the pterotic to its insertion on the antero-dorsal part of the operculum. *Levator* and *adductor* *operculi* muscles also originate from the pterotic and insert on the dorso-medial surface of the operculum.

The *levator arcus palatini* is a stout muscle originating from the pterotic and sphenotic, and inserting on the hyomandibula.

In *Nematogenys* (Nematogenyidae) the opercular muscles are complex, the *dilatator operculi* is large and plesiomorphic in its angle of insertion, i.e. postero-ventral, cf. the antero-ventral, apomorphic angle, in Loricariidae. The *levator operculi* inserts on the *lateral* face of the operculum; the *adductor operculi* is in its more usual position of the medial face. The *levator arcus palatini* is a large element with its lateral fibres interdigitating with the antero-ventral fibres of the *dilator operculi.*

In the Trichomycteridae the *dilatator operculi* is hypertrophied and is separable into lateral and medial parts. It originates from the underside of the frontal to pass beneath a sphenotic bridge where its lateral profile becomes convex before inserting on the lateral side of the long dorsally directed opercular process. The strap-like medial part of the muscle joins the medio-distal area of this process. The ventral portion of the *dilatator operculi* joins an aponeurosis with the dorso-posterior part of a muscle extending along the lateral face of the preoperculum. This muscle may be either a disassociated part of the adductor complex, or yet another segment of the *dilatator operculi* which has shifted ventrad.

The *levator* and *adductor operculi* also are hypertrophied and insert on the dorso-lateral and medial margins of the operculum respectively. The hypertrophy and lateral insertion of the *dilatator operculi* in the Nematogenyidae and the Trichomycteridae is viewed as synapomorphic – such a condition is unknown elsewhere in siluroids.

Interrelationships of loricariids based on myological characters

Although of restricted taxonomic range in terms of numbers of 'genera' examined (but, see below, p. 338), the anatomical data obtained from this investigation suffice to hypothesise phylogenetic relationships for the groups of loricariid genera. The scheme is based on what are considered to be derived states of jaw and opercular muscle characters. Two myological synapomorphies unite the Loricariidae and Astroblepidae as a monophyletic lineage; these are:

1. Presence of a medial muscle stemming from the suspensorium and inserting on the upper jaw (premaxilla). The muscle is recognized as a *retractor premaxillae* (p. 327).
2. Complete medial separation of the *protractor hyoideus* (p. 319). Within this lineage, the astroblepids retain a more generalized cranial muscle pattern and are considered to represent the plesiomorphic sister group to the loricariids. The loricariidae are defined myologically by the presence of a further medial adductor element inserting on the palatine (*retractor palatini;* p. 327) and by the orientation of the *dilatator operculi* which is angled antero-ventrally rather than postero-ventrally as in other siluroids and, indeed, other teleosts.

Within the Loricariidae, the following sequences of derived states in jaw and opercular muscles are discernible and are represented as a cladogram in Fig. 14.

1. *Dilatator operculi* angled antero-ventrally; *retractor palatini* present: LORICARIIDAE.
2. Reduction of opercular muscles and *levator arcus palatini.*
3. Lateral shift of *retractor tentaculi: Hypoptopoma, Otocinclus.*
4. Expansion of *retractor tentaculi: Chaetostoma, Lipopterichthys, Hemipsilichthys.*
5. *Retractor palatini* muscles meet in midline: *Loricaria* (part), *Farlowella, Sturisoma.*
6. Loss of *levator arcus palatini: Loricaria* (part).
7. Ventral division of *retractor tentaculi* inserts on palatine: *Loricaria* (part).
8. Loss of *levator* and *adductor operculi: Pseudohemiodon, Hemiodonichthys.*
9. *Dilatator operculi* originating from cranial roof, *levator operculi* from complex vertebrae: *Ancistrus, Lithoxus.*

10. Anterior shift of *dilatator operculi; adductor operculi* spans posttemporal-pterotic plate and preoperculum: *Panaque, Cochliodon, Stoniella, Pseudancistrus, Pseudacanthicus, Acanthicus.*

Because it is based on a single character complex, this synapomorphy scheme has limited information content and, for the most part, is a series of unresolved polychotomies. In order to test, and more fully resolve the scheme, various osteological characters have been utilised.

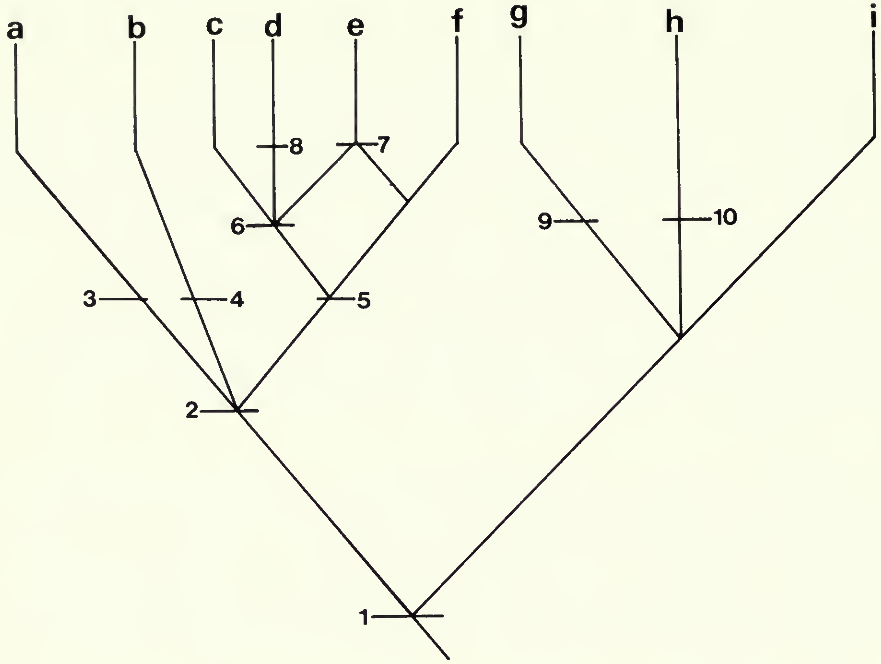

Fig. 14 Cladogram of loricariid taxa based on jaw and opercular muscle synapomorphies (see text, p. 329). a=*Hypoptopoma, Otocinclus*; b=*Chaetostoma, Lipopterichthys, Hemipsilichthys;* c=*Loricaria* (part); d=*Pseudohemiodon, Hemiodonichthys, Crossoloricaria;* e=*Loricaria* (part); f=*Farlowella, Sturisoma;* g=*Ancistrus, Lithoxus*; h=*Pseudacanthicus* group; i=*Hypoptostomus, Neoplecostomus. Pterygoplichthys.*

Congruent osteological features in Loricariidae

Four osteological characters are analysed. Three that are functionally integrated with the facial and opercular muscles, and one that has no direct relationship with the cranial musculature. They are: the lateral ethmoid; pterygoid channel; opercular bones and the lateropterygium of the pelvic girdle.

Lateral ethmoid and nasal capsule

Alexander (1965) noted that in most siluroids the nasal cavities are bounded medially by the ethmoid and posteriorly by the lateral ethmoid. In the majority of siluroids the palatine lies adjacent to the mesethmoid and contributes no part to the nasal cavity. In *Nematogenys,* (Nematogenyidae) the palatine is large and widely separated from the mesethmoid, forming an angle between the lateral ethmoid and the maxilla. The nasal cavity is thus bounded laterally by the palatine (Fig. 15B).

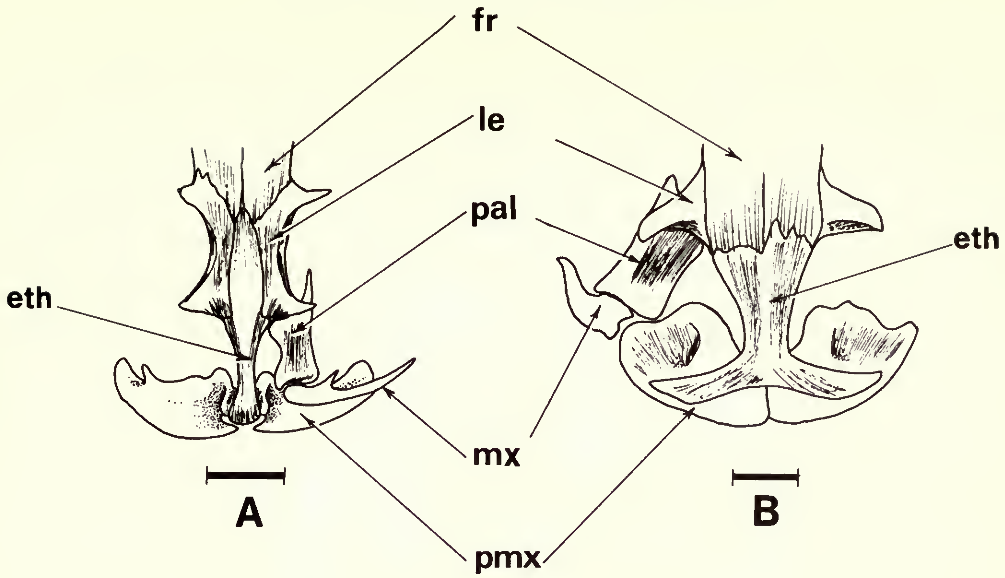

Fig. 15 Neurocrania, dorsal view of anterior region and upper jaw bones of A, *Astroblepus festae* (BMNH 1864.11.4:18); B, *Nematogenys inermis* (BMNH 1883.11.27:49). Scales = 5 mm. eth = ethmoid; fr = frontal; le = lateral ethmoid; mx = maxilla; pmx = premaxilla; pal = palatine.

Synapomorphic for *Astroblepus* (Astroblepidae) species is an expanded palatine which occupies the area between the lateral ethmoid and the mesethmoid. Its dorsal surface is excavated and accommodates the entire nasal capsule (Fig. 15A). Elsewhere this feature occurs only in *Trichomycterus rivulatus* (Trichomycteridae). If it is regarded as synapomorphic with that of *Astroblepus,* then the monophyly of *Trichomycterus* is in doubt.

In the Loricariidae the nasal capsule is contained within the lateral ethmoid. Entire encapsulation within the lateral ethmoid occurs also in the Callichthyidae (see Alexander, 1965). In some species of Doradidae and Auchenipteridae the posterior part of the nasal cavity is housed within the bone. Two conditions of encapsulation occur in loricariids; one in which the nasal cavity is incompletely walled and the other where the cavity is entire.

The former is exemplified by *Hypoptopoma* where the nasal cavity, whilst being entirely within the lateral ethmoid opens anteriorly as a shelf adjacent to the mesethmoid (Fig. 16A). The anterior border of the lateral ethmoid shelf meets the posterior border of the palatine. A similar situation occurs in *Sturisoma, Pterygoplichthys, Chaetostoma* (Fig. 18B), *Hemipsilichthys* and *Pseudacanthicus.* However, in all these taxa the anterior opening of the nasal cavity is partially occluded by a medially directed process extending from the lateral wall of the cavity (Fig. 16B). In *Ancistrus* the cavity is entire although a medially directed process protruding from its lateral wall is discernible (Fig. 17). The nasal cavity is entire in *Loricaria, Farlowella* (Fig. 18A) and *Neoplecostomus.*

The width of the anterior rim of the cavity is variable, being narrow in *Farlowella* and long and shelf-like in *Ancistrus* (Figs 17 and 18A). The length of the pre-nasal cavity part of the lateral ethmoid seems not to be coordinate with any elongation of the mesethmoid. Indeed, topographical relationship between the nasal cavity and its surrounding elements is maintained. In those taxa where there is mesethmoidal elongation, *Farlowella* and *Sturisoma,* there is no corresponding proportional lengthening of the lateral ethmoid. The lateral ethmoid serves as the site of origin for the *retractor tentaculi* muscle and it is likely that extension of the bone's surface area corresponds with hypertrophy of the muscle, as in *Chaetostoma.*

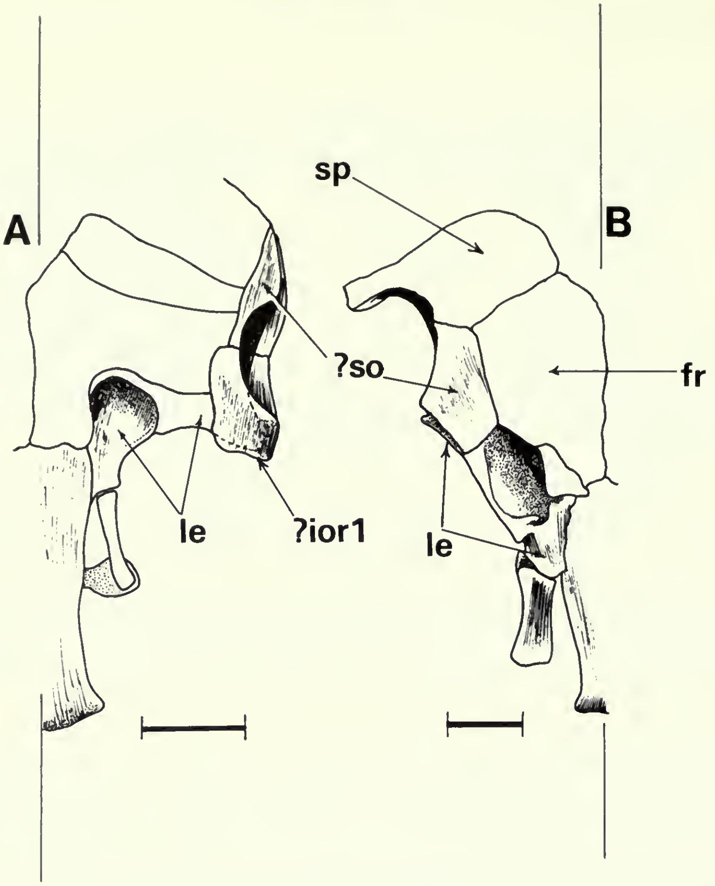

Fig. 16 Neurocrania, dorsal view of anterior and orbital regions of A, *Hypoptopoma carinatum* (uncat.); B, *Pterygoplichthys multiradiatus* (BMNH 1897.12.1:280). io = infraorbital; so = possible supraorbital. Scale = 5 mm.

In *Hypoptopoma* and *Otocinclus* the lateral ethmoid margin is extended laterally with the consequence that the *retractor tentaculi* muscle is also shifted laterally with respect to the other adductor muscles. Unlike other loricariids, the eyes in these genera are entirely lateral. It may be mentioned here that Gosline (1947) appears to have confused epidermal plates with neurocranial elements. His figures of the skull of *Hypoptopoma* show a 'dermosphenotic' lying *lateral* to the nasal cavity, i.e. forming the *anterior* border of the true neurocranium. In fact Gosline's 'dermosphenotic' is the lateral ethmoid, and the unlabelled bone shown lateral to it is perhaps the 1st infraorbital (Fig. 16A). It is also pertinent to draw attention to a dermal bone in some loricariids lying in the position of a supraorbital. One defining character of siluroid fishes is that they lack a supraorbital; see Fink & Fink, 1981.

A naive hypothesis to account for the position of the nasal cavity in the lateral ethmoid would be to assume, during phylogeny, a posterior migration of the nasal organ from its plesiomorphic position, adjacent to the anterior mesethmoid, *via* an anterior lateral ethmoid bridge. There is no extant 'transitional series' to indicate that this was the phylogenetic history of the nasal cavity shift. On the contrary, development of an anterior extension to the lateral ethmoid appears to be an apomorphic feature connected with the *retractor tentaculi* muscle, rather than indicating a plesiomorphic retention of the pathway along which the nasal organ shifted. Indeed, in assumed plesiomorphic members of the Loricariidae, e.g. *Neoplecostomus,* the nasal cavity is entirely enclosed within the lateral ethmoid.

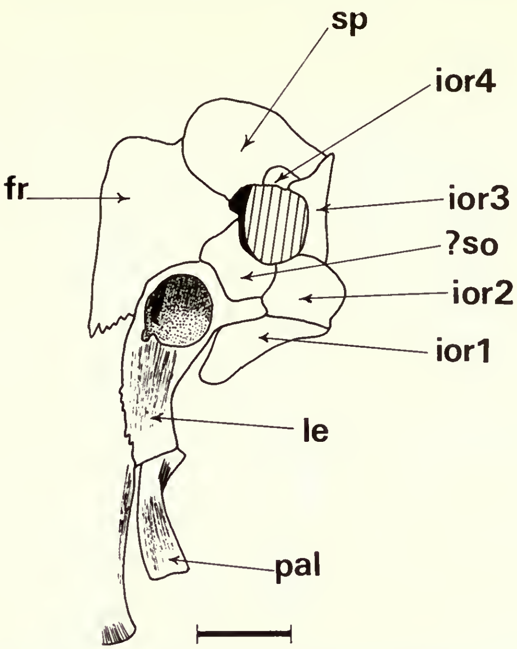

Fig. 17 Neurocranium dorsal view of anterior and orbital regions of *Ancistrus stigmaticus* (BMNH 1901.5.8:10). Scale = 5 mm. Abbreviations as in previous captions.

In *Astroblepus* the lateral ethmoid has a plesiomorph otophysan morphology i.e. short, and triangular; see Fink & Fink, 1981; Howes, 1981. The morphology and position of the palatine is, however, derived and might be viewed as the precursory condition of nasal organ reorientation in loricariids. This hypothesis is refuted, however, by the essentially plesiomorphic rod-shaped morphology of the palatine in the Loricariidae.

In the Callichthyidae the nasal organ is also enclosed within a cavity in the lateral ethmoid. Unlike the loricariids, the nasal cavity is well-separated from the mesethmoid, which is short and triangular, regarded as plesiomorphic in otophysans; see Fink & Fink, 1981; Howes, 1981. A superficial investigation of callichthyid osteology indicates that the lateral ethmoid encapsulation of the nasal organ has been derived independently from that in loricariids. More detailed studies of callichthyid and loricariid osteology are necessary before the feature can be accepted as a synapomorphy.

Pterygoid channel

In the Loricariidae the *extensor tentaculi* muscles originate from the lateral face of the pterygoid. The term 'metapterygoid' is avoided here as the elements of the siluroid suspensorium appear to have been misinterpreted by several authors (see Howes, 1983). The pterygoid in loricariids contacts the lateral ethmoid along its anterior length. In some taxa there is a pterygoid ridge or channel and it is the medial face of this ridge that provides the site of origin for the outer *extensor tentaculi* muscle, muscle **e** in the above text. In its more derived state, the pterygoid ridge extends dorsally to contact the lateral ethmoid and so completely encloses the *extensor tentaculi* in a tunnel.

A pterygoid ridge is weakly developed in *Pseudacanthicus, Stoniella* and *Acanthicus*; well-developed in *Pseudancistrus, Hemipsilichthys, Lipopterichthys* and *Chaetostoma,* and tunnel-like in *Ancistrus, Pterygoplichthys, Panaque* and *Farlowella.* In *Hypostomus* and *Cochliodon,* the anterior and posterior parts of the ridge are produced dorsally, with con-

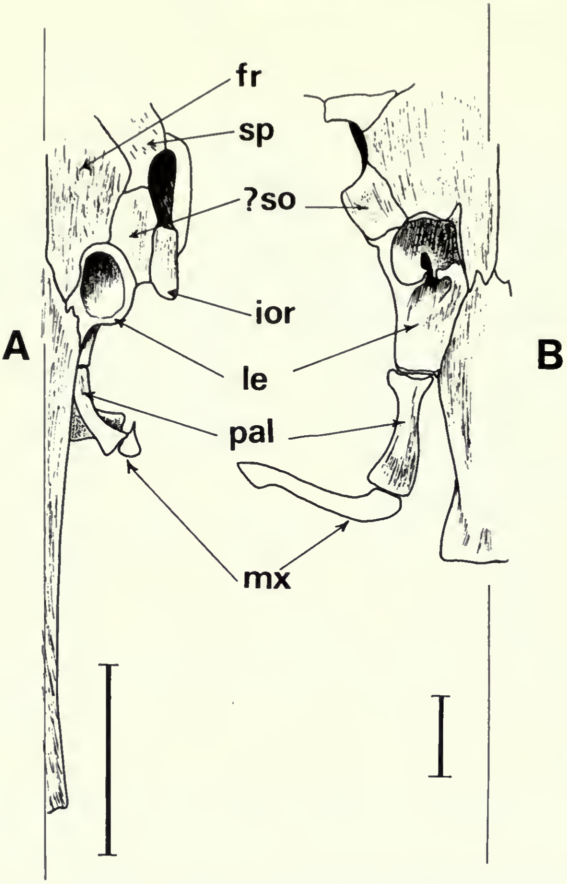

Fig. 18 Neurocrania, dorsal view of anterior and orbital regions of A, *Farlowella knerii* (BMNH 1880.12.5: 206); B, *Chaetostoma anomalus* (BMNH 1903.6.30:102). Scales = 5 mm. Abbreviations as previous captions.

nective tissue covering the intervening concavity. No development of the ridge is evident in *Hypoptopoma, Otocinclus, Loricaria, Sturisoma, Pseudohemiodon* and *Neoplecostomus*.

In the Astroblepidae and Nematogenyidae, the pterygoid is extensive, and in astroblepids its posterior margin, the 'metapterygoid' is sutured with the hyomandibula, as it is in loricariids. There is no lateral pterygoid ridge present in either family.

The pterygoid channel character states are incongruent with the cladogram of muscle characters. If the presence of a pterygoid ridge-tunnel is accepted as a synapomorphy, then that lineage containing *Chaetostoma* and *Hemipsilichthys* must be closely united with that represented by *Hypostomus*. So too, must *Farlowella* be united with *Ancistrus*. These seem unlikely combinations in the light of other synapomorphies (p. 338) and the most parsimonious explanation is to accept the pterygoid channel as having been derived independently in several lineages.

The opercular series

Some loricariid genera possess a mechanism whereby the spine-bearing 'interoperculum' can be rotated outward and the spines produced horizontally. Gosline (1947) was unable to find an interoperculum in *Ancistrus* and was of the opinion that what had been referred to as that bone was a patch of dermal plates. Gosline was only partially correct. He is certainly right that in *Ancistrus* the spine-bearing element does not appear to be the interoperculum but a partially ossified ligament. None the less, this ligament actually connects the operculum with the interoperculum which is immovably sutured to the preoperculum. A similar situation is present in *Pseudacanthicus* (Fig. 19B).

In *Chaetostoma* the situation is quite different. Here, the interoperculum is completely movable and articulates with the condyle of the opercular ventral extension (Fig. 19A). It is ligamentously attached to the preoperculum. In all taxa with a spine-erecting mechanism the operculum is elongate with an antero-ventral extension. There are, however, marked

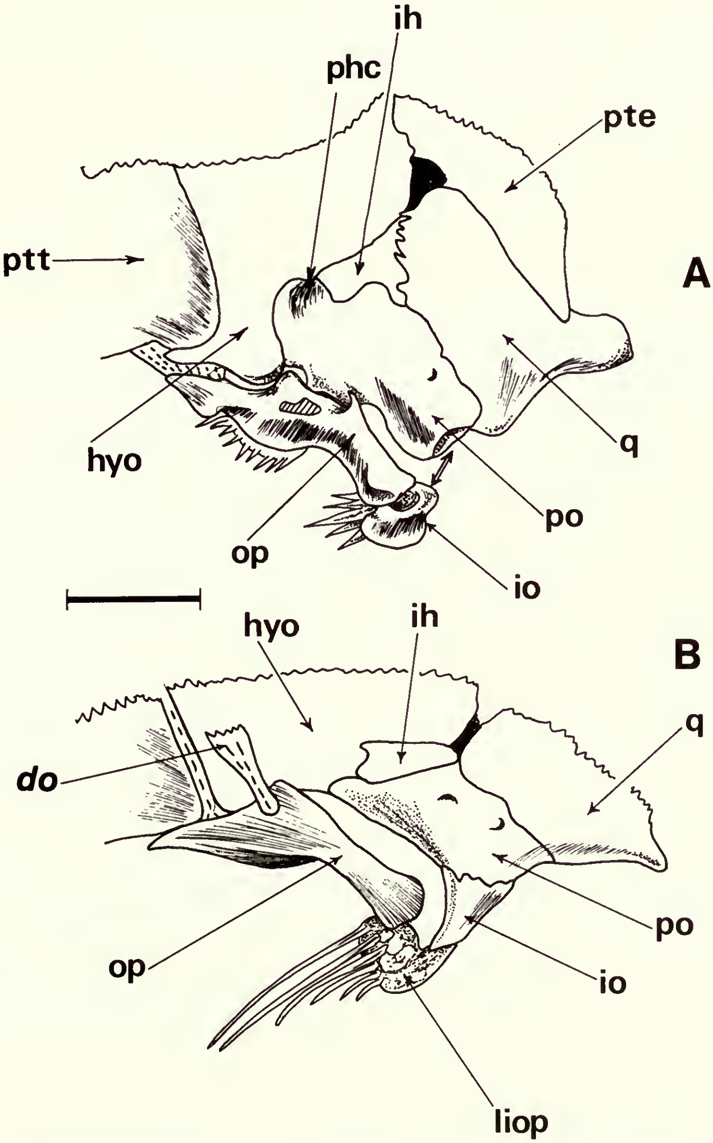

Fig. 19 Pterygoid and opercular bones in medial views of A, *Chaetostoma anomalus*, B, *Pseudacanthicus serratus*. The hatched portion of the operculum in A indicates the insertion area of the *dilatator operculi* muscle. hyo = hyomandibula; ih = interhyal; io = interoperculum; liop = interopercular-opercular ligament; op = operculum; phc = pterygoid cavity for interhyal; po = preoperculum; pte = pterygoid; ptt = posttemporal-pterotic plate; q = quadrate.

differences in morphology distinguishing two groups of taxa. In *Pseudacanthicus, Ancistrus* and *Lithoxus* there is a single articulation of the operculum with the hyomandibula at the point of the *dilatator operculi* muscle insertion. In *Chaetostoma* and *Lasiancistrus* there is a double articulation, one with the hyomandibular condyle and the other, *via* a dorsal process, with the medial surface of the preoperculum (Fig. 19A). These two groups of taxa also differ in the topographical arrangement of the suspensorial bones (cf. Figs. 19A & B). From these observations it is suggested that the 'interopercular' spine-erecting mechanism has been derived independently in two lineages of loricariids.

In some Trichomycteridae there is also an antero-ventral process of the operculum which articulates with a socket on the medial face of the spine-bearing interoperculum, e.g. *Branchioica, Pareiodon.* If the Trichomycteridae is a monophyletic assemblage (see remarks on p. 331 concerning the genus *Trichomycterus*) then it is clear that a similar mechanism to that of loricariids is the result of parallelism (*sènsu* Holmes, 1980: 49). The function of interopercular spines is discussed on p. 343.

The lateropterygium

In the Loricariidae and Astroblepidae the pelvic girdle bears a lateral, anteriorly directed process named by Regan (1904) a 'rudimentary ventral ray' and by Shelden (1937) a 'lateropterygium', the name adopted here. The lateropterygium articulates in condylar fashion with the lateral process of the basipterygium and is anchored laterally *via* a ligament to an adjacent body scute.

Shelden (1937) made a thorough study of the morphology of the lateropterygium as well as the pelvic muscles in *Astroblepus* and various loricariids. He found that in *Farlowella* a lateropterygium was lacking, a condition Shelden thought might be an artefact of preparation. I can confirm that this is not an artefact and that the lateropterygium is absent also in *Loricaria, Sturisoma, Hemiodonichthys* and *Pseudohemiodon.* As these taxa are admitted within the Loricariidae on the basis of other synapomorphies, e.g. specific form of scute development; structure of swimbladder encapsulation; caudal fin skeletal morphology and jaw musculature, the absence of a lateropterygium is viewed as a secondary loss in this lineage, = Loricariinae.

In the Astroblepidae, the lateropterygium is a disc-like plate and the basipterygium has posteriorly directed, elongate processes. The lateropterygium in Loricariidae varies from short and broad, as in *Neoplecostomus,* to long and rod-shaped as in *Pterygoplichthys.* There are no posterior processes of the basipterygium.

Regan (1904) considered the lateropterygium to be a rudimentary anterior ventral fin ray which had become '. . . internal and directed forwards'. Shelden (1937) on the other hand, thought the element to be homologous with the lateral cartilage in other siluroids.

Arratia *et al.* (1978) discussed the lateropterygium and the 'pelvic splint' in *Nematogenys* and the Trichomycteridae. They concluded that the elements are not homologous. However, they then considered that as neither lateropterygium nor pelvic splint has been recorded from other siluroids this was '. . . evidence of some relationship between these groups of South American fishes', thus implying homology. These authors further confuse the issue by referring to the primitive nature of the 'pelvic splint' on the grounds of its occurrence in 'lower' teleosts (*vide* Patterson, 1964).

A pelvic splint occurs in many characoids and cyprinoids and from its shape and position appears to be homologous with that similar element in other teleosts (Patterson, 1964: 444). Among siluroids a supplementary pelvic element is recorded only in the Trichomycteridae, Astroblepidae, Nematogenyidae, Loricariidae and Diplomystidae. In the Trichomycteridae the morphology of the bone is similar to that in other otophysans except that it is associated with the pelvic musculature and is detached from the first pelvic ray (see Arratia *et al.,* 1978).

Within the Loricariidae, the lateropterygium appears in its simplest form in the Hypoptopominae where in *Otocinclus* it resembles the pelvic splint of trichomycterids and diplomystids but, unlike the conditions in those taxa, it is orientated antero-dorsally instead of latero-posteriorly. This condition suggests that the lateropterygium is a pelvic splint which has become reorientated and articulated with the pelvic bone (as suggested by Regan, 1904; see above). Thus, the lateropterygium would be the homologue of the pelvic splint (rudimentary spine) in other teleosts, but its peculiar nature and articulation with the pelvic bone is a derived condition limited to the Loricariidae and Astroblepidae only.

Gosline (1974) was of the opinion that the lateropterygium was not a 'good classifying character, and that its presence, size and shape depend more or less on the extent of the plating of the sides and abdomen'. There must, as Gosline suggests, be a correlation between body shape, scute morphology and the development of the lateropterygium. Nevertheless, the presence and similarities of the bone in various taxa must indicate a shared ancestral condition. Thus, it is hypothesised that especially elongate rod-like lateropterygia are derived, whereas the short, broader morphology represents the plesiomorph condition.

Shelden (1937) concluded from his study of loricariid pelvic girdle morphology that *Ancistrus* and *Farlowella* represented two separately advanced states, a conclusion supported by this study. Shelden accounted for the function of lateropterygium as increasing the manoevrability of the pelvic girdle.

Myological + osteological characters

Utilizing derived character states from both myological and osteological complexes detailed above, together with those already noted in the literature (particularly Gosline, 1947), the following scheme of relationships is hypothesized and shown in Fig. 20.

1. Lateropterygium present	Astroblepidae + Loricariidae
2. *Retractor premaxillae* muscle present	
3. *Protractor hyoideus* muscle medially divided	
4. Nasal capsule confined to palatine	Astroblepidae
5. Gill-rakers absent	
6. Lateropterygium disc-like	
7. Lack of hyomandibulae fossae	Loricariidae
8. Nasal capsule confined to lateral ethmoid	
9. *Dilatator operculi* muscle antero-ventrally orientated; *retractor palatini* muscle present	
10. Body encased in scutes	
11. Reduction of opercular muscles, *dilatator operculi* confined to hyomandibula (*Neoplecostomus*)	*Neoplecostominae*
12. Expansion of *retractor tentaculi* muscle	Chaetostominae
13. Reduction of posterior cranial elements (e.g. supraoccipital, posttemporal-pterotic plate)	
14. Jaws lengthened and widened	
15. Lateral cheek spines (*Hemipsilichthys*)	
16. Interopercular spine mechanism (*Chaetostoma, Lasiancistrus, Lipopterichthys*	
17. The single character uniting *Hypoptopoma* and *Otocinclus* with the loricariine genera is the midline contact of the ventro-lateral scutes between the anus and anal fin origin (Gosline, 1947: 96) *versus* a single, azygous preanal plate in other loricariids. Synapomorphic for this lineage is the lateral position of the *retractor tentaculi*. On the basis of the characters used, it is not possible at this point to resolve a trichotomy of the neoplecostomine-chaetostomine-hypoptopomine (loricariine) lineages.	Hypoptopominae

18. *Retractor palatini* muscles meet in the midline
19. Caudal peduncle depressed, caudal vertebrae elongated, lateral scutes reduced.
20. Lateropterygium lost.
21. 'Adipose' fin lost; reduction of caudal fin ray number (10–14). These characters are of dubious value; the 'adipose' fin is also absent in some neoplecostomines, but it is noted here because of its complete absence in all loricariine taxa; the caudal fin ray number may be reduced in other lineages but appears consistently so in loricariines.
22. Mesethmoid elongated (*Sturisoma* + *Farlowella*)
23. *Extensor tentaculi* muscle enclosed in pterygoid tunnel (*Farlowella* + *Loricaria platystoma*); tendon of *retractor ischii* muscle runs through body-armour canals (*Farlowella*; see Shelden, 1937: 63).
24. Palatine lamellate, usually convex; 3rd, 4th and often 5th ceratobranchials expanded (?all taxa)
25. Ventral part of *retractor tentaculi* inserts on palatine (*Loricaria*, part)
26. Postorbital notch
27. Jaw teeth reduced or absent (*Loricaria*, part)
28. Palatine laterally compressed, *extensor tentaculi* inserts on its mid-ventral border; papillae developed over pterygoid. (*Pseudohemiodon, Hemiodonichthys*)

Loricariinae

29. Lower pharyngeal bones edentulous (?all taxa; see Gosline, 1947: 86)
30. Lateropterygium well-developed
31. Pterygoid channel or tunnel (*Hypostomus, Pterygoplichthys, Cochliodon*)
32. Pseudointeropercular mechanism entirely or partially developed (*Peckoltia, Hemiancistrus*)
33. Anterior shift *dilatator operculi* medial to orbit, *adductor operculi* bridges posttemporal-pterotic plate and preoperculum; upper jaw reduced, premaxillae coalesced (*Panaque, Stoniella, Pseudacanthicus, Acanthicus, Pseudancistrus*)
34. *Dilatator operculi* originates from cranial roof, *levator operculi* from complex vertebrae; *levator arcus palatini* joins tendon of *dilatator operculi*. (*Ancistrus, Lithoxus*)

Hypostominae

The cladogram constructed from nested sets of myological and osteological characters is, for the most part, congruent with that constructed from myological characters alone. It will be necessary to utilize other character sets, particularly those involving the morphology of the gill-arches, swimbladder encapsulation and the pectoral girdle in order to more highly corroborate this proposed phylogeny.

Classification of Loricariidae

The most recent synopsis of the Loricariidae is that of Isbrücker (1980) wherein are recognized six subfamilies, the Neoplecostominae, Lithogeneinae, Hypostominae, Ancistrinae, Hypoptopominae and Loricariinae. The genera included in these subfamilies follows, for the most part, those of Gosline (1947), Isbrücker, however, retains Regan's (1904) concept of the Neoplecostominae as monotypic by referring to it only *Neoplecostomus*, whereas Gosline has included 12 genera in the subfamily. Few representatives of those genera recognised by Gosline have been available for my study and their placement in one or other of the subfamilies recognised here is open to question. I have recognised *Neoplecostomus* as a sole representative of the Neoplecostominae purely on its retention of plesiomorph characters.

In the cladistic scheme presented in Fig. 20 the major lineages are equivalent to subfamilies and the included taxa are broadly those currently contained in the Hypostominae, Hypoptopominae and Loricariinae. Genera formerly incorporated in the Ancistrinae are here divided between the Hypostominae and Chaetostominae = Chaetostomidi, Fowler, 1958. No speci-

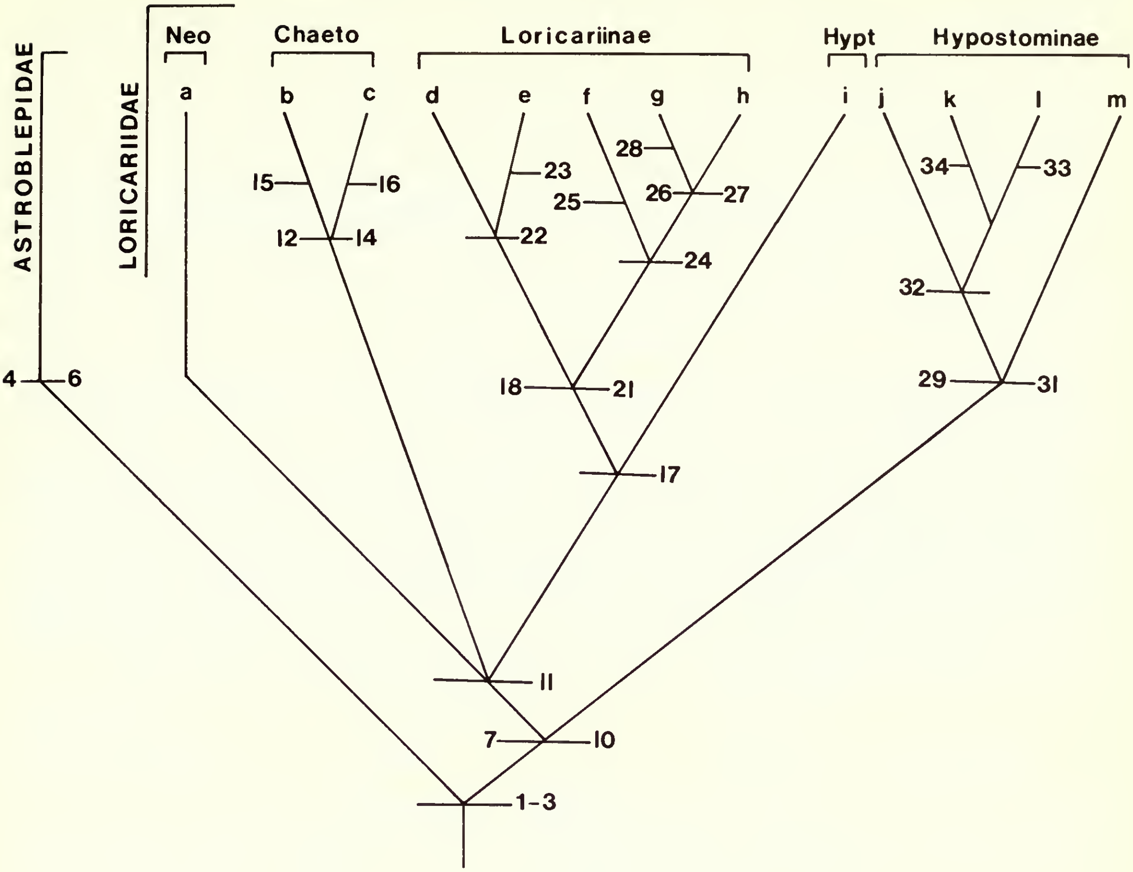

Fig. 20 Cladogram of the Astroblepidae and Loricariidae based on muscle and skeletal synapomorphies (see text, p. 337). a = *Neoplecostomus* (Neo = Neoplecostominae); b = *Hemipsilichthys*, c = *Chaetostoma, Lasiancistrus, Lipopterichthys*, (Chaeto = Chaetostominae); d = *Sturisoma*; e = *Farlowella*; f = *Loricaria* (part, *strigilata, simillima*), *Metaloricaria*; g = *Pseudohemiodon, Hemiodonichthys, Crossoloricaria;* h = *Loricaria* (part, e.g. *cataphracta*); i = *Hypoptopoma, Octocinclus, Parotocinclus, ?Microlepidogaster*, (Hypt = Hypoptopominae); j = *Pekoltia, Hemiancistrus*; k = *Ancistrus, Lithoxus*; l = *Panaque, Stoniella, Pseudacanthicus, Acanthicus, Pseudancistrus;* m = *Hypostomus, Pterygoplichthys, Cochliodon.*

mens of *Lithogenes* have been examined and thus no comment can be made concerning the status of the monotypic subfamily Lithogeneinae.

Isbrücker (1980) lists 70 loricariid genera; it is likely that many are synonyms, particularly those recognised on the basis of single specimens. It is pertinent to note that of the 70 genera, 21 are monotypic and so might merely reflect the generic concepts of their respective authors. The characters used to define many loricariid genera appear to depend on meristic and dental differences, varying numbers of body scutes and lower lip morphology. Most of these characters appear to be gradal. A character that appears to be significant in the classification of *Loricaria* species is the presence in some of a posterior orbital notch or fossa. The fossa is variously developed, varying from a slight indentation to a deep, medially directed channel. There is no organ or vessel contained within the fossa and it is floored with connective tissue. Its function is unknown but may serve to enlarge the posterior visual field. Presence of a post-orbital fossa is regarded as synapomorphic for those *Loricaria* species in which it occurs. In a sample of 16 species belonging to 7 'genera' the following distribution of the fossa is recorded:

Absent: *Crossoloricaria, Spatuloricaria, Loricaria, Loricariichthys*
Slightly developed: *Paraloricaria, Loricaria, Ricola*
Well developed: *Rineloricaria, Loricaria, Loricariichthys*

One genus, *Loricaria,* appears in all three morpho-groups and *Loricariichthys* appears in two. This result indicates that the present generic classification of the Loricariinae is possibly a paraphyletic one. In support of this statement I find that in *Loricaria sensu stricto* as represented by the type species, *L. cataphracta,* the *retractor tentaculi* muscle inserts partly on the palatine (see p. 315). This feature is restricted to those taxa which lack the post-orbital fossa, or at best have it slightly developed, e.g. *'Limatulichthys' punctatus; 'Pseudoloricaria' laeviuscula.*

Other characters which override current generic allocations of loricariine species are the ligamentous suspension of the upper jaw, the length of the lateral ethmoid and morphology of the palatine.

There are two basic types of ligamentous jaw suspension in *Loricaria,* (1) where the maxilla is attached to a ventral process of the vomer *via* a single, folded ligament; there is also a small rostral cartilage, and (2) where there are several ligaments connecting the maxilla with the vomer and there is a large rostral cartilage (Figs 21A & B). The former type of jaw suspension is present in *Loricaria labialis,* assigned by Isbrücker to *Loricariichthys, L. cataphracta, Sturisoma, Farlowella* and *Hemiodonichthys.* The latter occurs in *Loricaria jubata* and *L. brunneus* which Isbrücker refers to *Rineloricaria* and *Loricariichthys* respectively.

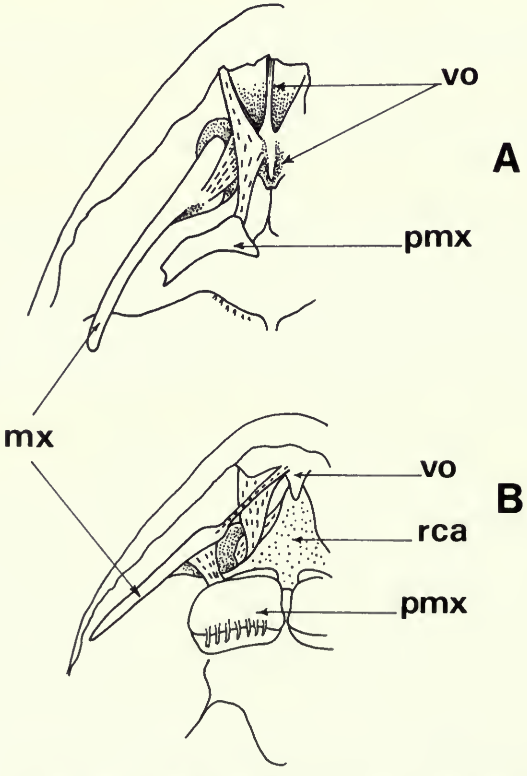

Fig. 21 Ligamentous connections of the upper jaws in A, *Loricaria labialis* (BMNH 1934.8.20: 368–388) and B, *L. jubata* (BMNH 1914.5.18: 68–72). Ventral views, both drawn to same scale. mx = maxilla; pmx = premaxilla; rca = rostral cartilage; vo = vomer.

The length of the lateral ethmoid and morphology of the palatine in *Loricaria* species are perhaps correlated. For example, in *L. cataphracta,* the lateral ethmoid is long and shelf-like, the palatine narrow and lamellate with a long posterior process whereas in '*Rineloricaria' teffeana* the lateral ethmoid is short and broad and the palatine is also short and broadly convex, lacking a posterior process.

Isbrücker (1981) in discussing the Loricariini notes that there are '... several different types of secondary sexual dimorphism ...' within the group. If this is so, then here is a further indication of the group's paraphyly.

Discussion

The interrelationships of the Loricariidae

In the latest classification of the order Siluroidei, Chardon (1968) includes the Loricariidae, Astroblepidae and Callichthyidae in the superfamily Loricarioidae within the suborder Loricarioidei. Chardon recognises two other superfamilies as constituting the suborder, the Aspredinoidae and the Trichomycteroidae.

It is doubtful that the aspredinids are closely related to the loricariids and trichomycterids. Chardon used an assortment of apo- and plesiomorph characters involving the swimbladder and Weberian apparatus to unite his groups. There are marked differences in the structure of the swimbladder-Weberian system between the Aspredinidae and the Loricariidae as follows:

	Aspredinidae	*Loricariidae*
Swimbladder	Not encapsuled	encapsuled
Anterior centra	Elongate	short
4th parapophysis	Short	contributes to swimbladder capsule

On the other hand, there are several synapomorphies of the swimbladder-Weberian system and caudal fin skeleton that link the Loricariidae with the Astroblepidae and Callichthyidae (see Alexander, 1964, 1965; and Lundberg & Baskin, 1969; also below).

As noted above p. 323 the astroblepines have been variously treated as a subfamily of the Loricariidae (Regan, 1911; Gosline, 1947) and as a distinct family (Eigenmann, 1910). There is no doubt that on the basis of synapomorphies presented here the astroblepines must be treated as the sister group to the Loricariidae. Following Chardon's (1968) scheme of classification both families would form the super-family Loricarioidae — this is not, however, in accordance with the cladistic scheme presented in Fig. 22.

Bailey & Baskin (1976) described a new taxon which they regarded, provisionally as a subfamily of the Loricariidae, the Scoloplacinae. The authors pointed out that its inclusion in the family would necessitate a 'significant expansion' of the Loricariidae. Baskin's (1973, unpublished) cladogram places *Scoloplax* as the sister group to the Loricariidae + the Astroblepidae, i.e. at family rank. With this I would concur and also follow Isbrücker (1980) in recognising the Scoloplacidae.

The pattern of phylogenetic relationships between the Loricariidae + Astroblepidae and the Nematogenyidae, Trichomycteridae, Callichthyidae and Scoloplacidae has still to be resolved. Baskin (1973, unpublished thesis) has produced a phylogenetic scheme which is essentially like that presented here (Fig. 22). There are, however, several conflicting presumed synapomorphies not taken into account by Baskin. For example the Nematogenyidae shares only with the Trichomycteridae a derived configuration of the opercular musculature (p. 329), but shares only with the Diplomystidae a similarly papillate branchiostegal membrane and buccal roof tissue. Again, the Callichthyidae shares what appear to be derived features of swimbladder encapsulation with the Astroblepidae, Loricariidae and Scoloplacidae, but a premaxillary-ethmoid hinge joint only with the two former families. Lateral ethmoid encapsulation of the nasal organ occurs only in the Loricariidae and Callichthyidae.

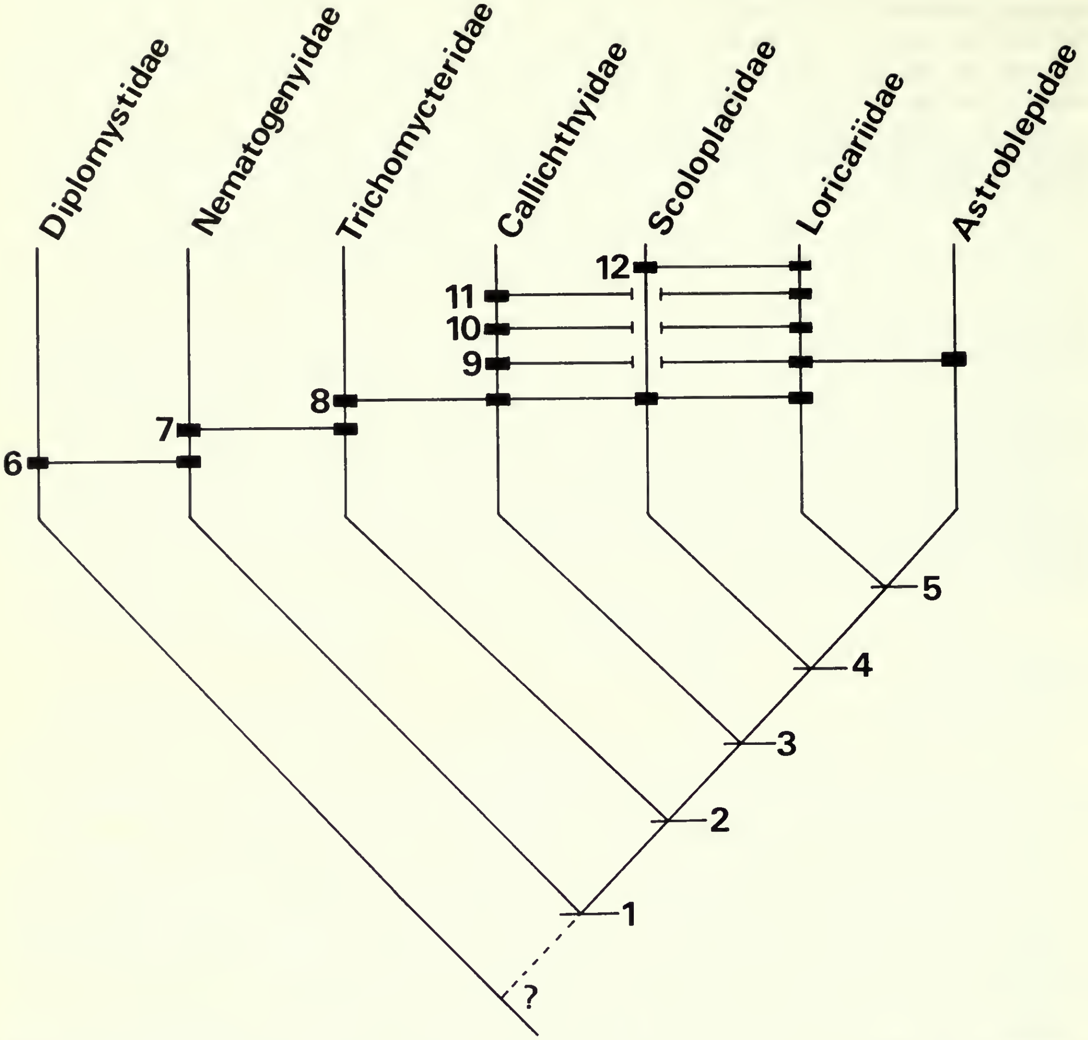

Fig. 22 Hypothesised relationships of the Loricariidae and Astroblepidae. Node 1 = swimbladder encapsuled, divided into separate vesicles; some part of the cranium contributing to encapsulation; odontodes on fin rays and/or body. Node 2 = Claustrum and intercalarium lacking from the Weberian vertebral series. Node 3 = Posttemporal contributing to distal portion of the swimbladder capsule; derived hypural fusion pattern; low number of principal caudal fin rays. Node 4 = connecting bone between the 1st rib and the 2nd pterygiophore. Node 5 = muscle characters listed in this paper, associated with reverted lip; lateropterygium (see p. 336; 6 fused anterior centra. Line 6 = papillate branchiostegal membrane and buccal roof tissue. Line 7 = lateral insertion of the *dilatator operculi* muscle. Line 8 = odontodes on opercular bones. Line 9 = Ethmoid-premaxillary hinge joint. Line 10 = nasal organ encapsuled in lateral ethmoid. Line 11 = rows of lateral plates partly or entirely encasing body. Line 12 = rostal epidermal ossifications bearing odontodes.
Characters 6–12 are incongruent with 1–5 and so indicate either independent derivation (9, 10 in Callichthyidae) or secondary loss (8, 11, 12 in Astroblepidae).

The characters listed above are compiled from Gosline (1947), Lundberg & Baskin (1969), Bailey & Baskin (1976), Baskin (unpublished thesis, 1973) and personal observation.

The absence in the Astroblepidae of certain characters linking the Loricariidae, Scoloplacidae, Callichthyidae and Trichomycteridae (i.e. opercular odontodes, body plates) is most parsimoniously explained by secondary loss (see opinions of Bhatti, 1938 and Gosline, 1947 concerning loss of armour in *Astroblepus*).

As yet, comparative anatomical studies on the various genera presently included in the Callichthyidae are lacking. Such data as are available are summarized in the cladistic scheme presented here (Fig. 22).

Functional considerations

Several pointers have emerged in the course of this study as to the functional significance of certain myological features. In particular, the medially divided *protractor hyoideus* signifies independent mobility of the separate halves of the lower jaw. Aquarium observations on a variety of loricariid taxa have confirmed this (pers. obs.). The *intermandibularis* is only weakly attached to the two halves of the mandible and the bulk of the muscle runs through the lip tissue. It would appear that in loricariids the principal function of the muscle is to activate the lip as a sucker. Alexander (1965) has given an account of lip movement associated with respiration.

The diversity of jaw morphology ranges from long, broad upper and lower jaws (*Chaetostoma*) to the short, deep inwardly curved lower jaw and coalesced, almost circular, upper jaw of *Pseudacanthicus*. In both morphotypes the jaws appear highly mobile, but the angles of their respective muscle insertions indicate quite different manipulative abilities.

In astroblepids and loricariids, the upper jaw is free from the restraint imposed by the ankylosed mesethmoid, common to the majority of siluroids. Only in callichthyids has the upper jaw a similar, ligamentous, attachment to the mesethmoid, although here its vertical rotation appears limited through firm attachment to the palatines.

The palatine appears to play a somewhat different functional role in loricariids as compared with other siluroids. Its lack of firm attachment to the ethmoid seems to impart a greater degree of mobility to the bone, and the postero-ventral attachment of part of the *extensor tentaculi* muscle provides a degree of downward movement lacking in other siluroids. This is particularly marked in the *Pseudohemiodon* group where the *extensor tentaculi* has shifted its position to the centre of the centre of the palatine and there is a tendinous palatine-maxillary-premaxillary linkage (see Fig. 5B).

An inferior, sucker-like mouth comparable with that of loricariids occurs elsewhere amongst siluroids in the African genus *Euchilichthys* and the Asian *Glyptothorax* and *Glyptosternon*. In these taxa the muscular insertions to the upper jaw differ from those in loricariids in that the *retractor tentaculi* inserts for the most part on the premaxilla with a tendinous outer portion running to the maxilla. The palatine is short and is actuated by an *extensor tentaculi* passing into its medial face. The premaxilla is overlapped by an anterior extension of the mesethmoid and appears to have less mobility than in loricariids.

As noted above, p. 342, loricariids and their relatives have a head and body covering of odontodes and in some taxa these have become elongate and collected in certain areas to form clumps of spines. The spines are of two kinds, those that are embedded in the cheek tissue to which the pediments are attached by ligament (see Bhatti, 1938) and those that are attached to the interoperculum, embedded in small plates. Both types of spine can be shed; according to Moodie & Power (1982), in *Loricaria uracantha*, cheek spines develop over a 64 day period and are lost within 148 days. Scars on the interoperculum of male *Chaetostoma* specimens indicate that the spines have been shed (pers. obs.). Allison, (1980; pers. comm.) reports aquarium observations on the use of interopercular spines in *Ancistrus* sp. When two males sight one another their initial reaction is to open the interopercular flap and evert the spines rapidly on both sides simultaneously. If one or other fish remains undeterred a ‘combat’ situation develops with the individuals aligning themselves side by side, everting their opposing spines (those on the blind side remaining withdrawn) and engaging them by sideways movements of the head. These movements are made by strong lateral curvatures of the caudal peduncle and tail. These observations suggest that at least in *Ancistrus* the interopercular spine function is one of display. It is noted that the spines are not as well-developed in females of *Ancistrus* who nevertheless do display their spines by lateral movements when approached by conspecifics whilst feeding (Allison, pers. comm.).

The fixed cheek spines of *Hemipsilichthys* and various *Loricaria* species is also a sexually dimorphic character. In males the cheeks are fringed with long, closely packed spines, whilst those of the females bear small, widely spaced spines. Moodie & Power (1982) report on the use of pectoral fin and cheek spines in *Loricaria uracantha* where the male has the ability to rotate forward its pectoral spines so that they lie adjacent to the cheek spines and so probably act as clasping organs during spawning.

According to Eigenmann (1918) trichomycterids use their opercular spines as holdfasts to the substrate. The same function would seem to operate in parasitic trichomycterids, the only difference being the nature of the substrate. Such may be the plesiomorph function of the interopercular spines in loricariids. Aquarium observations suggest that some loricariids use their spines to secure a position in the substrate (Allison, pers. comm.; pers. obs.).

The *dilatator operculi* muscle is well-developed only in those taxa with a pseudointeropercular spine erecting mechanism, *Ancistrus, Pseudacanthicus* etc., and its role in activating the operculum in respiratory movements seems restricted. Respiratory activity probably falls largely on the *adductor hyohyoidei* which extend well up the medial face of the operculum. Often the last branchiostegal ray is attached to the opercular face by the musculature or at least an intervening tissue fascia. The tight seal of the operculum to the cleithrum also suggests its rather passive role in respiration.

Acknowledgements

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Dr Ethelwynn Trewavas

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Three genera of the mouth-brooding species are included though in one of them, *Danakilia*, the single species is too small to warrant farming. The other two, *Sarotherodon*, with nine species, and *Oreochromis*, with thirty-one, are distinguished primarily by their breeding habits and their biogeography, supported by structural features. Each species is described, with its diagnostic features emphasised and illustrated, and to this is added a summary of known ecology and behaviour. Conclusions on relationships involve assessment of parallel and convergent evolution. Dr Trewavas writes with the interests of the fish culturists, as well as those of the taxonomists, very much in mind.

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A lectotype for *Deuterammina (Deuterammina) rotaliformis* (Heron-Allen & Earland) and new trochamminids from E. Ireland (Protozoa: Foraminiferida)

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Introduction

In their 'Report on some Recent Foraminifera found off the coast of Dublin and in the Irish Sea', Balkwill & Wright (1885) illustrated four views, two umbilical and two spiral (pl. 13, figs 11a, b and 12a, b) of agglutinating foraminifera which they refer to as *'Trochammina inflata* Montagu sp. var.'; no formal description was given. Twenty-six years later Heron-Allen & Earland (1911 : 309) encountering in shore sands of Selsey Bill, Sussex, a single trochamminid which they regarded as identical with that reported by Balkwill & Wright, sent it to Joseph Wright in Ireland for a second opinion. Wright indeed agreed with their identification. In their paper, Heron-Allen and Earland cite it as *'Trochammina rotaliformis* J. Wright MS' and write '... as Mr. Wright will, we understand, describe and figure the variety shortly under the name *rotaliformis,* we refrain from further particulars of the variety which has not hitherto been accorded a distinctive name, although presenting well-marked characteristics'. Wright did not publish this description, but Heron-Allen & Earland by referring to Balkwill & Wright's figures, while citing Wright's manuscript name, themselves made the name available. Article 12 of the International Code of Zoological Nomenclature states 'that names published before 1931 ... must have been accompanied by a description, definition or indication [Art. 16]'; an indication being constituted under Article 16a (i) by 'a bibliographic reference to a previously published description, definition or figure'. An 'indication' was therefore clearly given, furthermore, Heron-Allen and Earland are the authors of the name, not Wright, with 1911 being the date of availability (R. V. Melville, pers. comm.). This is contrary to subsequent references to the species as *'Trochammina rotaliformis* J. Wright MS' by Heron-Allen & Earland (1913), Cushman (1920), and in the Catalogue of Foraminifera (Ellis & Messina, 1940 *et seqq.*).

Cushman (1920 : 77, pl. 16, figs 1, 2) re-illustrated Balkwill & Wright's four figures, and at the same time made the first formal description of the species...

> Test small, trochoid, spire somewhat elevated, composed of about three volutions, gradually increasing in diameter; chambers distinct, four in each volution, sutures oblique and curved, slightly depressed, ventral side irregular, the last formed chamber occupying nearly one-half the area of the test, smoothly finished; aperture elongate, at the base of the chamber in the umbilical region, with a sort of lip-like projection above; color reddish or yellowish brown. Diameter, up to 0·45 mm.

He however omitted to select a type-specimen, which is unfortunate, for as will be seen three of the four individuals illustrated by Balkwill & Wright (and Cushman), though of similar size are morphologically distinct, belonging even to separate genera. As long as the species

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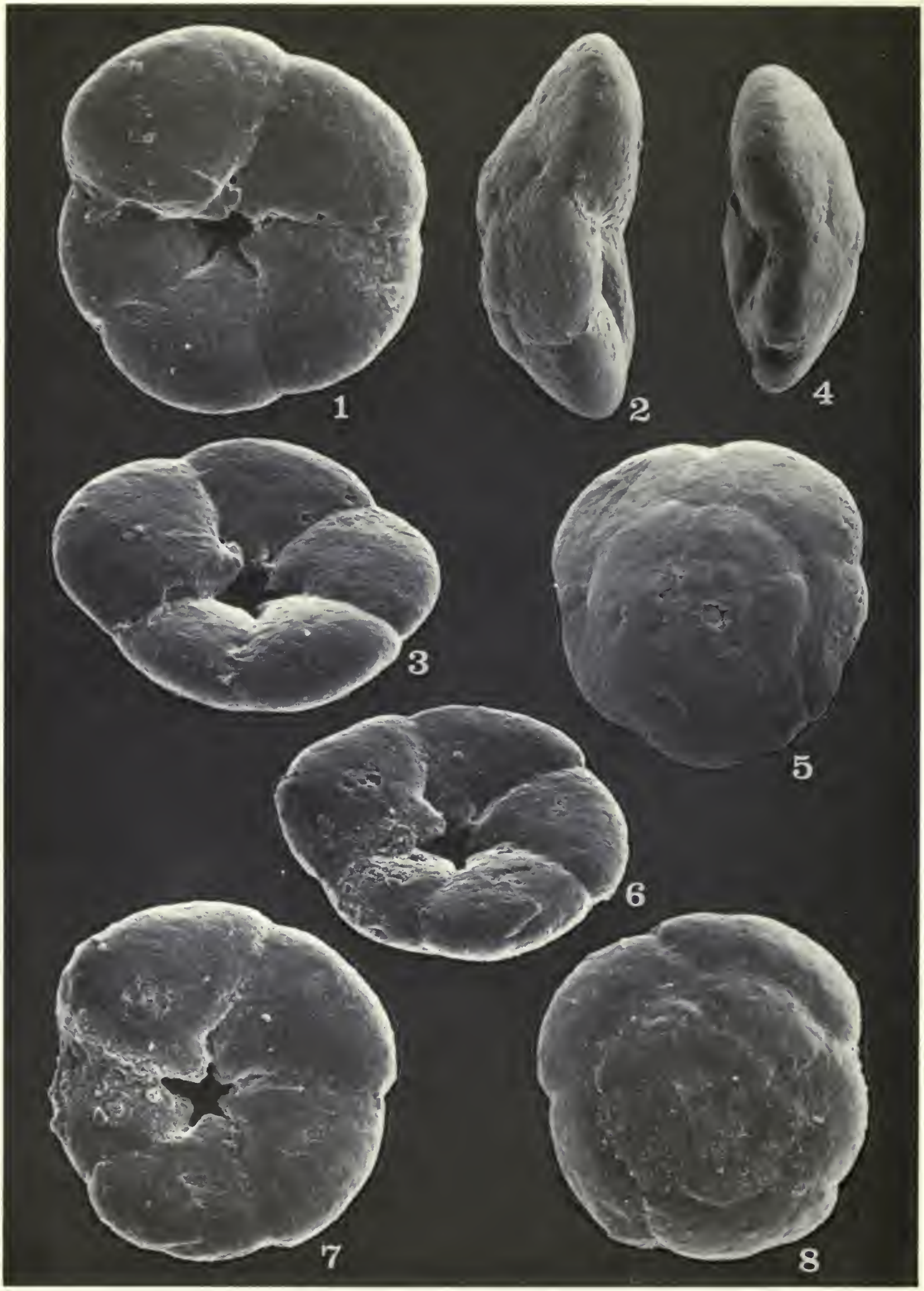


Figs 1–8 *Deuterammina (Deuterammina) rotaliformis* (Heron-Allen & Earland). Figs 1–3, Lectotype (N.M.I. no. 1.1980). Umbilical, edge and oblique-umbilical views. Specimen figured by Balkwill & Wright, 1885, pl. 13, fig. 12b. Figs 4, 5 Paralectotype (N.M.I. no. 2.1980). Edge and spiral views. Figs 6–8, Paralectotype (N.M.I. no. 3.1980). Oblique-umbilical, oblique and spiral views. All from Killiney Bay, E. Ireland, 8–14 fathoms (15–25 m). Ex Wright collection (13–1921), labelled *Trochammina inflata* var., ×220.

lacked a type-specimen, no clear morphological concept existed and hence subsequent workers interpreted *T. rotaliformis* differently, for instance Höglund (1947), Murray (1971), and Todd & Low (1981).

In order to stabilize the concept of *T. rotaliformis* Heron-Allen & Earland, its morphological features need to be determined on the basis of a lectotype. Then, and only then can this species be properly identified and used meaningfully in taxonomic and ecological work.

At first glance Cushman's description (1920: 77) of *T. rotaliformis* apparently refers to the slightly smaller specimen shown in Balkwill & Wright's drawings (1885, pl. 13, fig. 11b) by an umbilical view, because he mentions four chambers per whorl and that the final chamber occupies nearly half of the umbilical side. Other features of this description referring to the spiral side, the aperture and the smoothly finished surface, on the other hand, seem to be derived from the other three specimens shown in the original illustrations (pl. 13, figs 11a; 12a, b) which clearly are morphologically different from the first mentioned individual. Cushman apparently regarded, as did Balkwill & Wright, the four specimens as conspecific. The supposition is confirmed by the grouping of Balkwill & Wright's four figures in Cushman's pl. 16—as fig. 1 (putting erroneously together as belonging to the same form, their original figs 12a and b) and, as fig. 2 (doing the same for their figs 11a and b). Cushman's description is therefore a composite one.

Recently Balkwill & Wright's figured specimens have been found in the National Museum of Ireland (N.M.I.) preserved in the Joseph Wright Collection (13–1921) and in the light of the above confusion, it is opportune to select a lectotype and describe the species afresh. Of their figured material, those specimens representing pl. 13, figs 11b, 12a and 12b (1885) have been photographed using a Scanning Electron Microscope and are re-illustrated by our respective Figs 1–3, 25 (=fig. 12b); Figs 13–16, 26 (=fig. 12a) and Figs 17–20, 27 (=fig. 11b). The specimen shown in their fig. 11a has not been scanned; it has, we can confirm, the same umbilical features as that shown in fig. 12b.

Our micrographs clearly demonstrate that the original illustrated specimens were not conspecific, but in fact belong to three different species which are placed according to their apertural characteristics into the genera *Deuterammina (Deuterammina)* (Balkwill & Wright, 1885, pl. 13, figs 11a; 12a, b) and *Paratrochammina (Paratrochammina)* (figs 11b).

We designate Balkwill & Wright's specimen N.M.I. 1.1980, shown originally in umbilical view (fig. 12b) as lectotype of *D. (D.) rotaliformis* (Heron-Allen and Earland). Their fig. 11a is also conspecific and as it is by far the commonest form in the material labelled '*T. inflata* var.' or '*T. rotaliformis* MS' in the Wright Collection from E. Ireland, it would therefore seem the logical choice. The remaining two specimens from the original figured material are described as *D. (D.) balkwilli* (=fig. 12b) and *Paratrochammina (P.) wrighti* (=fig. 11b), while a further species has been isolated in Wright's faunal slide collection labelled as *T. rotaliformis*. Previously not illustrated, it has distinctive apertural characters and is described as *Deuterammina (Centrodeuterammina) dublinensis* subgen. et sp. nov.

Systematics

The specimens illustrated in this paper are deposited in the National Museum of Ireland, Dublin, and registered as 1.1980–3.1980 and 107.1981–111.1981, inclusively.

Genus ***DEUTERAMMINA*** Bronnimann, 1976, emended Brönnimann & Whittaker, 1983

Subgenus ***DEUTERAMMINA*** Brönnimann, 1976

TYPE-SPECIES. *Trochammina glabra* Heron-Allen & Earland, 1932.

Deuterammina (Deuterammina) rotaliformis (Heron-Allen & Earland)
(Figs 1–8, 25)

1885 *Trochammina inflata* (Montagu) var. Balkwill & Wright (*pars*): 331, pl. 13, figs 11a, 12b only.
1889 *Trochammina inflata* var. Balkwill & Wright (*sic*); Halkyard: 63, pl. 1, fig. 10.

1892 *Trochammina inflata* (Montagu) var. Balkwill & Wright; Chaster: 58.

1911 *Trochammina rotaliformis* J. Wright MS: Heron-Allen & Earland: 309 (availability of name).

1920 *Trochammina rotaliformis* J. Wright; Cushman (*pars*): 77, pl. 16, fig. 1 (right). 2 (left) only. [After Balkwill & Wright, 1885].

1973 *Trochammina astrifica* Rhumbler; Haynes (*pars*): 34, pl. 4, fig. 18 only (*non Trochammina squamata* Jones & Parker *astrifica* Rhumbler, 1938).

1974 *Trochammina rotaliformis* Wright; Lévy *et al*: pl. 1, figs 4, 5.

MATERIAL. 9 syntypes, 3 from Killiney Bay, 6 from off Drogheda, E. Ireland. Wright Collection (13–1921), National Museum of Ireland (N.M.I.), Dublin.

LECTOTYPE. N.M.I. no. 1.1980, from slide labelled *Trochammina inflata* var., Killiney Bay, E Ireland, long. 6°8′W, lat. 53°15′N, depth 8–14 fathoms (15–25 m). Specimen figured by Balkwill & Wright, 1885, pl. 13, fig. 12b. Refigured in Figs 1–3, 25.

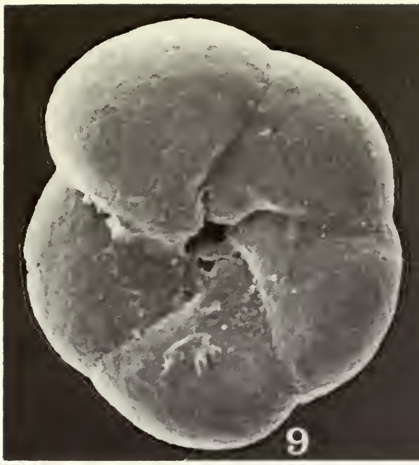
DESCRIPTION (LECTOTYPE). Test free, a low dextral trochospire, subcircular in umbilical and spiral views and slightly lobate. In edge view, broadly domed on the spiral side though somewhat flattened axially; shallow-concave umbilically; periphery sharply rounded, but not carinate. Umbilical depression star-shaped, open and deep with five branches. On spiral side, small subglobular proloculus followed by about 20 chambers arranged in at least three whorls with five chambers in the final whorl. Radial and spiral sutures not well defined in the early volutions and thus exact numbers of chambers difficult to determine. In final whorl, slightly curved intercameral sutures are but little depressed spirally; rather more so on umbilical side. Septum not infolded. Umbilically, shape of chamber broadly triangular; spirally, low and elongate. Two sets of apertures consisting of an interiomarginal extraumbilical primary opening of *Trochammina*-type and a secondary opening in a umbilical-sutural, posteriorly directed position. Secondary openings lead directly into the umbilicus and probably remain functional throughout ontogeny. Primary openings, on the other hand, not in direct connection with umbilical depression, only the last-formed connecting with the exterior. Final primary opening devoid of any lip-like structure but secondary openings accompanied by distinct extensions which normally are well separated from septal wall. Wall single-layered and imperforate. Agglutinant of quartz flakes arranged in mosaic-like pattern. Colour reddish brown.

DIMENSIONS (LECTOTYPE). Maximum spiral and umbilical diameter 260 µm, minimum diameter 230 µm; thickness (axial height) 100 µm. Maximum diameter of star-shaped umbilical depression 60 µm, length of each branch of star c.20 µm. Length and height of primary aperture, 27 and 9 µm respectively. Extension associated with secondary apertures (final chamber) 30 × 15 µm.

VARIATION (PARALECTOTYPES). 4 paralectotypes have been chosen from the remaining syntypic series, two each from Killiney Bay, and from off Drogheda, (long. 6°15′W, lat. 53°45′N), N.M.I. no. 2.1980, 3.1980, and 107.1981, 108.1981, respectively. Their overall morphology is similar to that of the lectotype, two are dextral, two, sinistrally coiled. All, together with the remaining unfigured specimens in the Wright Collection, are characterized by 5 chambers in the final whorl and by the same, 5-branched star shaped, open and deep umbilical depression, into which the secondary openings of the chambers of the final whorl lead under the hook-shaped lip-like extensions. Paralectotype 2.1980 (Figs 4, 5) is made up of about 20 chambers and a subglobular proloculus of about 10 µm diameter. The number of chambers of the spirally shown paralectotype (3.1980: Figs 6–8) cannot be determined, the early volutions being masked by foreign matter.

DIMENSIONS (PARALECTOTYPES)

	Diameter		Thickness
N.M.I. no. (Fig.)	Maximum	Minimum	(axial height)
2.1980 (Figs 4, 5)	240 µm	220 µm	100 µm
3.1980 (Figs 6–8)	220 µm	200 µm	—
107.1981 (Figs 9–11)	250 µm	220 µm	100 µm
108.1981 (Fig. 12)	230 µm	210 µm	—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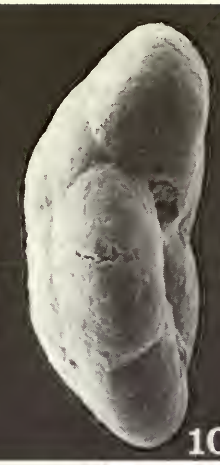
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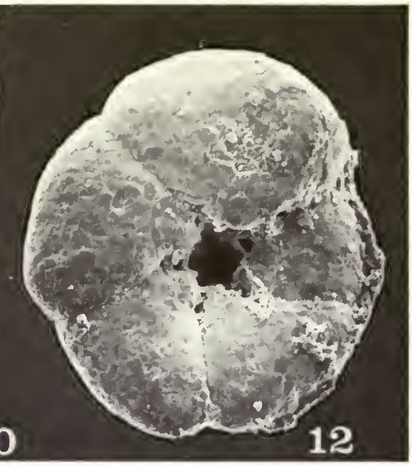
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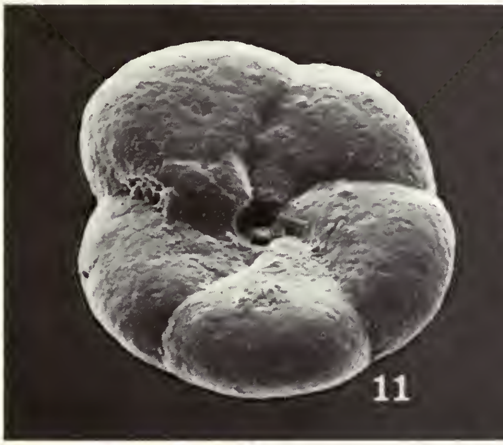
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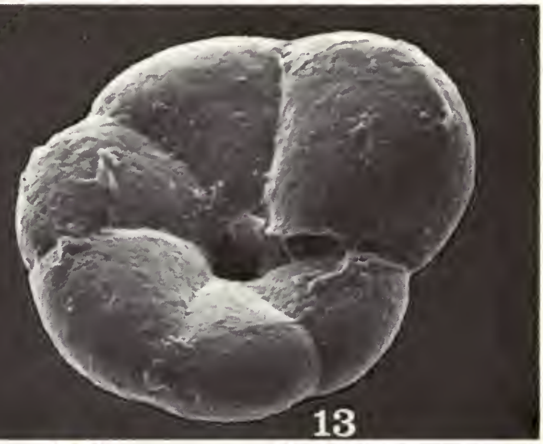
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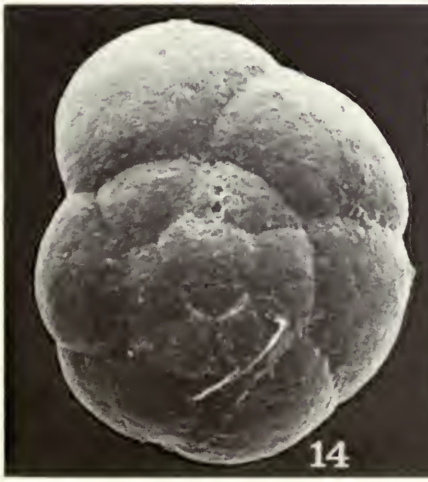
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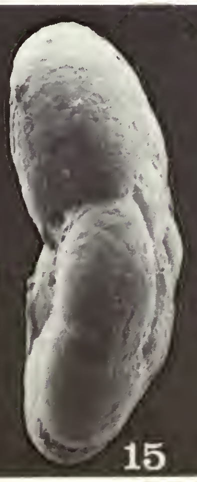
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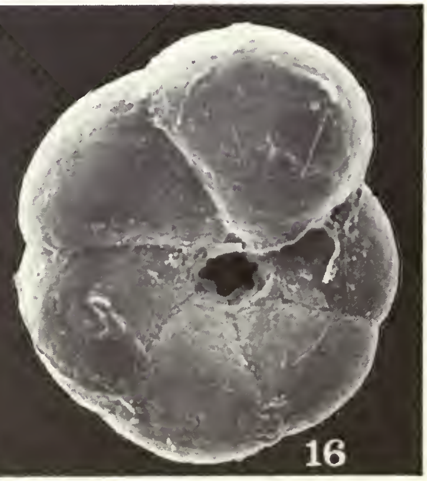
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Figs 9–12 *Deuterammina (Deuterammina) rotaliformis* (Heron-Allen & Earland). Figs 9–11, Paralectotype (N.M.I. no. 107.1981). Umbilical, edge and oblique-umbilical views. Fig. 12, Paralectotype (N.M.I. no. 108.1981). Umbilical view.
Both from off Drogheda, E. Ireland, 16 fathoms (30 m). Ex Wright collection (13–1921), faunal slide no. 34. ×220.

Figs 13–16 *Deuterammina (Deuterammina) balkwilli* sp. nov. Holotype (N.M.I. no. 109.1981). Oblique-umbilical, spiral, edge and umbilical views. Specimen figured by Balkwill & Wright, 1885, pl. 13, fig. 12a.
From Killiney Bay, E. Ireland, 8–14 fathoms (15–25 m). Ex Wright collection (13–1921), labelled *Trochammina inflata* var., ×220.

REMARKS. *D. (D.) rotaliformis* (Heron-Allen & Earland) has been compared with the deep-water deuteramminids found in the *Discovery* material from the S. Atlantic and Antarctic waters—*D. (D.) discorbis* (Earland), *D. (D.) glabra* (Heron-Allen & Earland), *D. (D.) grisea* (Earland) and other, so far undescribed species (Brönnimann & Whittaker, in preparation). It is easily distinguishable by its overall morphology, the position and shape of the primary aperture, plus the hook-shaped, lip-like extensions (see Fig. 25) under which the secondary openings occur.

D. (D.) rotaliformis under the name '*Trochammina rotaliformis* Wright' or 'Wright MS' is one of the most frequently cited taxons in the Trochamminidae, notwithstanding the fact that, lacking up till now a type specimen, no-one could have known its true morphology (Heron-Allen & Earland, 1916 : 228; 1922 : 114; 1932 : 344; Earland, 1933 : 85; 1934 : 99; Parr, 1950 : 276; Collins, 1958 : 354; and others). Furthermore in almost all cases where it has been illustrated (Heron-Allen & Earland, 1913 : 52, pl. 3, figs 11–13; Cushman & McCulloch, 1939 : 107, pl. 87, figs 2a–c; Cushman & Todd, 1947 : 7, pl. 1, fig. 14; Cushman, 1948 : 42, pl. 4, fig. 16; Todd & Low, 1967 : 418, pl. 1, figs 18a, b; 1981 : 18, fig. 49; Murray, 1971 : 39, pl. 12, figs 1–5; Van Voorthuysen, 1973 : pl. 13 (pl. 14 on plate explanation), figs 3a–c) it invariably does not correspond with the lectotype as selected in the present paper. Only two records subsequent to the original citation appear definitely conspecific; one is by Haynes (1973 : 34, pl. 4, fig. 18 (but not figs 19 and 20) who illustrated a specimen from Cardigan Bay, W. Wales (as *Trochammina astrifica* Rhumbler), which is typical of *D. (D.) rotaliformis*. The other is by Lévy *et al.* who illustrated (1974 : 128, pl. 1, figs 4, 5) from Dunkirk beach sand, N. France, an umbilical and spiral view, of the true *rotaliformis*. The umbilical view of their specimen, in particular, shows beautifully the double aperture.

Deuterammina (Deuterammina) balkwilli sp. nov.
(Figs 13–16, 26)

1885 *Trochammina inflata* (Montagu) var. Balkwill & Wright (*pars*): 331, fig. 12a only.

1920 *Trochammina rotaliformis* J. Wright; Cushman (*pars*): 77, pl. 16, fig. 1 (left) only. [After Balkwill & Wright, 1885].

?1971 *Trochammina rotaliformis* Heron-Allen & Earland; Murray (*pars*); 39, pl. 12, fig. 5 only.

DIAGNOSIS. A 6-chambered, compressed *Deuterammina.* Star-shaped umbilical depression small with 6 very short radial branches. Primary and secondary apertures poorly separated.

NAME. For F. P. Balkwill, co-author with J. Wright of the paper 'Recent Foraminifera off the coast of Dublin and Irish Sea', 1885.

MATERIAL. 1 specimen, ex J. Wright Collection (13–1921), National Museum of Ireland (N.M.I.), Dublin.

HOLOTYPE. N.M.I. no. 109.1981, from slide labelled *Trochammina inflata* var., Killiney, E. Ireland, long. 6°8′W, lat. 53°15′N, depth 8–14 fathoms (15–25 m). Specimen figured by Balkwill & Wright, 1885, pl. 13, fig. 12a. Refigured in Figs 13–16, 26.

DESCRIPTION (HOLOTYPE). Test free; a low sinistral trochospire consisting of about 16 axially compressed chambers arranged in 3 whorls with 6 chambers in the final whorl. Suboval in umbilical and spiral views and slightly lobate. In edge view, gently convex spirally and shallow-concave umbilically; periphery rounded. Umbilically, shape of chambers roughly triangular separated by almost straight sutures; spirally, chambers are elongate and relatively low, separated by curved sutures. Radial and spiral sutures well defined. Umbilical depression open and deep, characterized by star-shaped outline with 6 short radial branches, the result of incomplete overlap of the apertural rim of the primary aperture on that of the preceding chamber. Two sets of apertures consisting of primary interiomarginal opening in umbilical-extraumbilical position and a minute posteriorly directed secondary opening in sutural position, hence of *Deuterammina*-type. Primary opening an elongate slit accompanied by an upturned rim, the prolongation of the septal wall. It rests with its border on the first and penultimate chamber of final whorl (Figs 13, 26). Secondary openings not well-separated from large slit-like interiomarginal primary openings: however, recognizable as minute sutural slits between ends of apertural rims of primary openings and those of preceding chambers; they occur below proximal sides of radial branches and are posteriorly directed. All primary and secondary openings are in direct communication with the umbilical cavity and hence the exterior. Wall agglutinated, smooth, and apparently single-layered and imperforate. Surface appears finely granular on both sides, but granulation slightly coarser umbilically.

Dimensions (holotype). Maximum spiral and umbilical diameter 260 µm, minimum diameter 220 µm, thickness (axial height) 90 µm. Maximum diameter of star-shaped umbilical depression 40 µm, length of each branch of star c.10 µm. Length and height of primary aperture, 60 and 22 µm, respectively; width of apertural rim c.5 µm.

Remarks. *D. (D.) balkwilli* differs from *D. (D.) rotaliformis* (Heron-Allen & Earland) essentially in the apertural features. In the latter, the primary and secondary openings are separated, the secondary sutural, posteriorly directed openings are much longer and better developed than in *D. (D.) balkwilli.* As the primary and secondary openings in our new species cannot be clearly separated, except by assuming that the extent of the apertural rim marks the extent of the primary aperture, there is some evidence for a new subgeneric deuteramminid taxon distinct from *Deuterammina (Deuterammina)* Bronnimann, 1976 and *D. (Lepidodeuterammina)* Brönnimann & Whittaker, 1983. However, this would be premature with the material available. *D. (D.) balkwilli* has 6 chambers in the final whorl as against 5 in *D. (D.) rotaliformis* and a slightly different aspect in edge view. Murray's photograph (1974, pl. 12, fig. 5) of a six-chambered specimen of what he calls *Trochammina rotaliformis* Heron-Allen & Earland could be conspecific with ours. It is however only shown in edge view, the spiral and umbilical views are of different specimens and a different species (see p. 357 below).

Genus ***DEUTERAMMINA*** Brönnimann, 1976

Subgenus ***CENTRODEUTERAMMINA*** subgen nov.

Type species. *Deuterammina (Centrodeuterammina) dublinensis* Brönnimann & Whittaker, 1983.

Definition. Test free, trochospiral, low, but not 'watchglass' shaped. Wall agglutinated, single-layered, imperforate. Chambers axially compressed; without inner structures. Aperture double: primary opening interiomarginal, extraumbilical; secondary or supplementary opening at umbilical tip of chamber; directed centrally into umbilical cavity.

Name. Subgeneric name refers to centrally directed secondary opening.

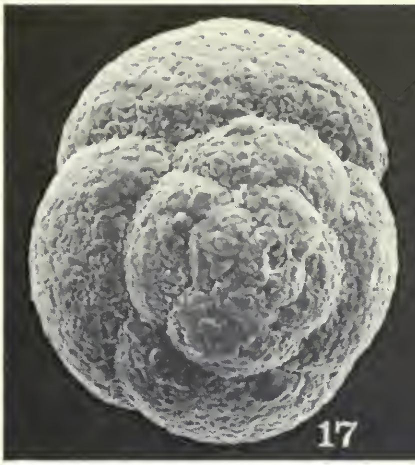
Remarks. *D. (Centrodeuterammina)* differs from *D. (Deuterammina)* and *D. (Lepidodeuterammina)* (see Brönnimann & Whittaker, 1983), both of which possess secondary openings posteriorly directed in an umbilical-sutural position. The secondary openings of *D. (Centrodeuterammina)* are centrally directed and occur at the umbilical tip of the chambers. *D. (Lepidodeuterammina)* differs further from both *D. (Deuterammina)* and *D. (Centrodeuterammina)* by the attached, 'watchglass' shaped test.

Deuterammina (Centrodeuterammina) dublinensis sp. nov.

(Figs 21–24, 28–30)

Diagnosis. A 7-chambered deteramminid, compressed in edge view; spiral side plano-convex. Strongly lobate in umbilical/spiral views, chambers slightly inflated, spiral and radial sutures well defined. Umbilical depression narrow and deep.

Name. After the type locality, Killiney Bay, near Dublin, Eire.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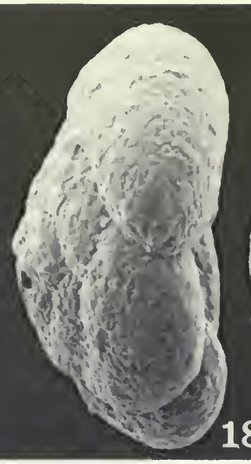
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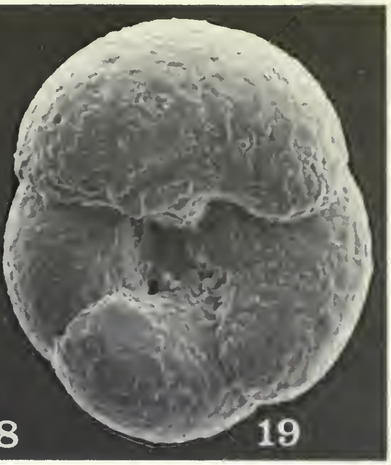
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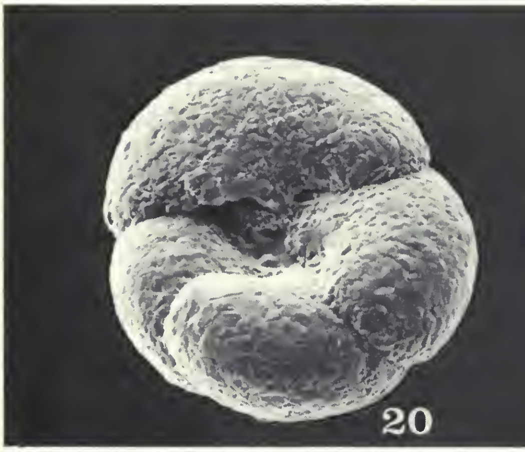
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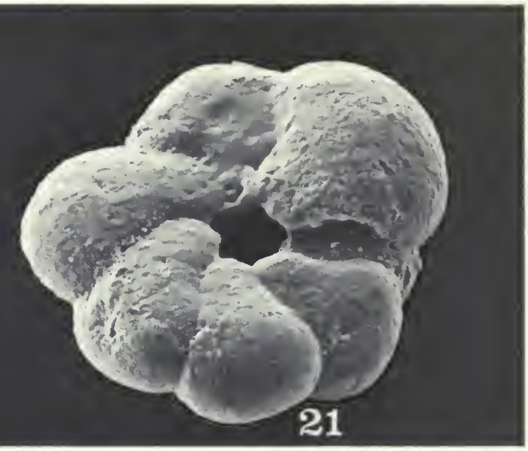
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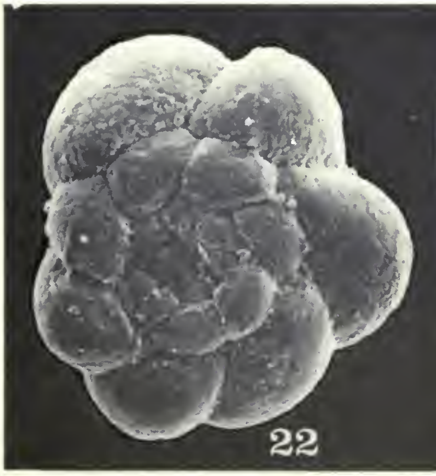
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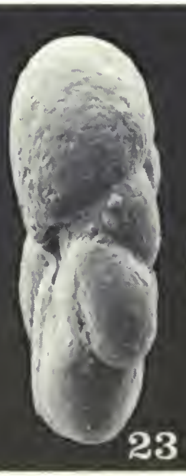
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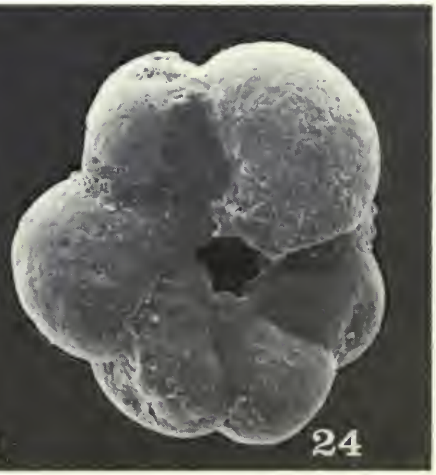
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Figs 17–20 *Paratrochammina (Paratrochammina) wrighti* sp. nov. Holotype (N.M.I. no. 110.1981). Spiral, edge, umbilical and oblique-umbilical views. Specimen figured by Balkwill & Wright, 1885, pl. 13, fig. 11b.
From off Drogheda, E. Ireland, 16 fathoms (30 m). Ex Wright collection (13–1921), labelled *Trochammina inflata* var., ×220.

Figs 21–24 *Deuterammina (Centrodeuterammina) dublinensis* subgen. et sp. nov. Holotype (N.M.I. no. 111.1981). Oblique-umbilical, spiral, edge and umbilical views.
From Killiney Bay, E. Ireland, 8–14 fathoms (15–25 m). Ex Wright collection (13–1921), faunal slide no. 27, ×220.

MATERIAL. 1 specimen, ex Wright Collection (13–1921), National Museum of Ireland (N.M.I.), Dublin.

HOLOTYPE. N.M.I. no. 111.1981, from faunal slide no. 27, Killiney Bay, E. Ireland, long. 6°08′W, lat. 53°15′N, depth 8–14 fathoms (15–25 m). Specimen illustrated in Figs 21–24, 28–30.

DESCRIPTION (HOLOTYPE). Test free, trochospiral; coil very low, sinistral, consisting of 20 chambers, including the proloculus, arranged in three whorls with 7 chambers in the last whorl. Chambers of at least the last two whorls, axially compressed. Subcircular in umbilical and spiral views and strongly lobate. In edge view, spiral side almost plano-convex, umbilical side shallow-concave, periphery rounded. Radial and spiral sutures slightly curved, in early whorls straight-oblique; umbilically, slightly sinuous. Umbilical depression narrow, deep, showing at the sutures short sutural branches formed by the overlap of the rims of the secondary umbilically-directed openings on those of the preceding chamber. Each chamber with two apertures: a primary interiomarginal opening in an extraumbilical position of *Trochammina*-type (that is with its borders resting completely on the wall of the first chamber of the final whorl) and a secondary opening at umbilical tip of chamber, directed into axial cavity. Primary apertures covered by succeeding chambers leaving only ultimate one to communicate directly with exterior, whereas all secondary apertures open into umbilical depression and remain functional. Primary interiomarginal opening an elongate slit devoid of any border lip but edged with granules (Fig. 28). Secondary openings arranged in a low trochospire within umbilical cavity (Fig. 30): in the early part of the coil, short and semicircular; final ones, elongate with more or less flat walls. Borders of early openings a series of discrete granules and flakes arranged more or less perpendicularly to the borders, later ones have thin walls devoid of granules. Agglutinated wall apparently single-layered and imperforate. Spiral side with granules, umbilical side with flakes and granules, the latter surface of distinctly coarser texture.

DIMENSIONS (HOLOTYPE). Maximum diameter in umbilical and spiral view 240 µm, minimum diameter 220 µm, thickness (axial height) 80 µm. Maximum diameter of umbilical cavity 40 µm. Length and height of primary aperture, 55 and 10 µm, respectively; ditto, secondary apertures (early coil), 10 × 5 µm.

REMARKS. This species was not figured by Balkwill & Wright, 1885, but was contained in Wright's faunal slide collection and from his MS identification was clearly considered by him to fall within the concept of *T. rotaliformis*.

Genus ***PARATROCHAMMINA*** Brönnimann, 1979 emended Brönnimann & Whittaker

EMENDED GENERIC DEFINITION. Test trochospiral, free. Wall agglutinated, single layered, imperforate. Chambers devoid of inner structures (septal infoldings). Aperture single, interiomarginal, umbilical-extraumbilical; border of opening resting on umbilical wall of first chamber of last whorl and on that of penultimate chamber; asymmetric in respect to axis of coiling, with or without an umbilical flap.

TYPE SPECIES. *Paratrochammina madierae* Brönnimann, 1979. Recent. South Atlantic (Brazilian Shelf).

Subgenera of *Paratrochammina*

In the present classification of the Trochamminidae only the position of the single interiomarginal aperture is accepted as a generic criterion. Because the presence of an umbilical flap can be variably developed this character is here reduced to second order of importance and, unlike formerly (Brönnimann & Whittaker, 1981), now accepted only as of subgeneric significance. The genus is divided into *P. (Paratrochammina)* and *P. (Portatrochammina)*.

Subgenus *PARATROCHAMMINA (PARATROCHAMMINA)* Brönnimann, 1979

SUBGENERIC DEFINITION. Aperture single, interiomarginal, umbilical-extraumbilical, border of opening rests on umbilical wall of first chamber of last whorl and on that of penultimate chamber; asymmetric in respect to axis of coiling; without umbilical flap.

TYPE-SPECIES. As genus.

Subgenus *PARATROCHAMMINA (PORTATROCHAMMINA)* Echols, 1971

SUBGENERIC DEFINITION. Aperture single, interiomarginal, umbilical-extraumbilical, border of opening rests on umbilical wall of first chamber of last whorl and on that of penultimate chamber; asymmetric in respect to axis of coiling, with umbilical flap more or less covering umbilical depression.

TYPE-SPECIES. *Portatrochammina eltaninae* Echols, 1971 (=*Paratrochammina (Portatrochammina) antarctica antarctica* (Parr, 1950). Recent. Soctia Sea, Antarctica.

Paratrochammina (Paratrochammina) wrighti sp. nov.
(Figs 17–20, 27)

1885 *Trochammina inflata* Montagu var. Balkwill & Wright (*pars*): 331, pl. 13, fig. 11b only.

?1913 *Trochammina rotaliformis* J. Wright MS; Heron-Allen & Earland: 52, pl. 3, figs 11–13.

1920 *Trochammina rotaliformis* J. Wright; Cushman (*pars*): 77, pl. 16, fig. 2 (right) only. [After Balkwill & Wright, 1885].

?1971 *Trochammina rotaliformis* Heron-Allen & Earland; Murray (*pars*): 39, pl. 12, figs 1–4 only.

DIAGNOSIS. A 4-chambered paratrochamminid. In edge view, convex spirally, shallow-concave umbilically. Chambers 'broad bean' shaped, spiral and radial sutures well defined. Central umbilical depression shallow, aperture with small lip-like plate.

NAME. After Joseph Wright, co-author with F. P. Balkwill of the first and only comprehensive and illustrated account of the foraminifera of the western Irish Sea.

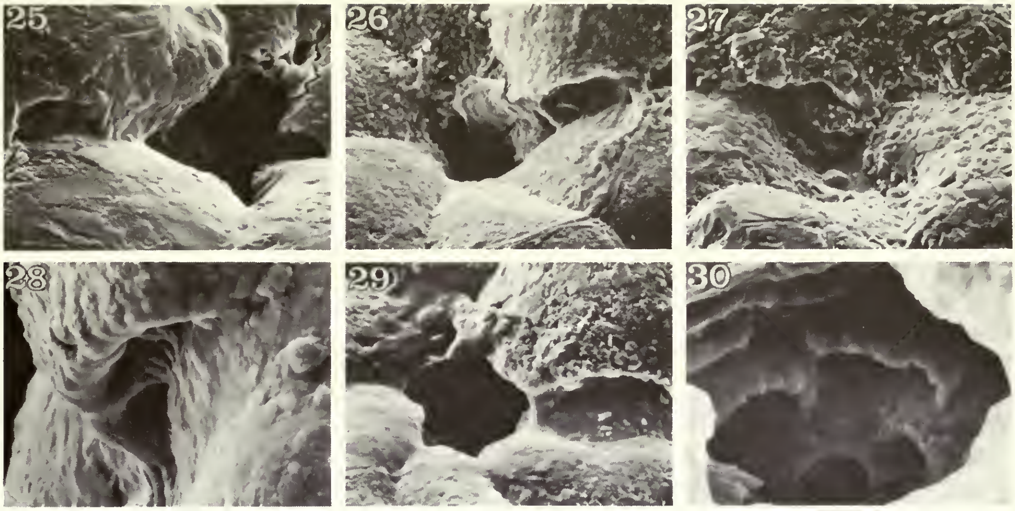
MATERIAL. 1 specimen, ex Wright Collection (13–1921), National Museum of Ireland (N.M.I.), Dublin.

HOLOTYPE. N.M.I. no. 110.1981, from slide labelled *Trochammina inflata* var., off Drogheda, E. Ireland, long. 6°15′W, lat. 53°45′N, depth 16 fathoms (30 m). Specimen figured by Balkwill & Wright, 1885, pl. 13, fig. 11b. Refigured in figs 17–20, 27.

DESCRIPTION (HOLOTYPE). Test free, trochospiral; coil moderately low, dextral, consisting of 13 chambers arranged in three whorls, with four chambers in final whorl and at least in last two whorls axially compressed. Broadly oval in umbilical and spiral views. In edge view, convex spirally, obtusely pointed axially; shallow-concave umbilically; periphery rounded. Chambers 'broad bean' shape umbilically, elongate crescentic spirally. Radial and spiral sutures well-defined. Intercameral sutures strongly curved spirally and somewhat sinuous umbilically. Umbilical depression, shallow, open. Single interiomarginal aperture of crescentic shape with central lip-like plate. Border of aperture rests on wall of first and third chamber of final whorl (of *P. (Paratrochammina)* type). Agglutinated wall appears single-layered and imperforate. Surface, fairly rough, composed of flakes and grains of rock fragments; texture of spiral surface coarser than umbilical.

DIMENSIONS (HOLOTYPE). Maximum spiral and umbilical diameter 250 μm, minimum diameter 220 μm, thickness (axial height) 120 μm. Maximum diameter of umbilical depression c.50 μm. Length of aperture 90 μm, length and width of apertural plate 50 and 9 μm, respectively.

REMARKS. The single *Paratrochammina*-type aperture readily distinguishes this species from the deuteramminids described above, all with double apertures. The central lip-like apertural



Figs 25–30 Apertural detail. Fig. 25, *Deuterammina (Deuterammina) rotaliformis* (Heron-Allen & Earland). Lectotype (N.M.I. no. 1.1980). Oblique view showing primary and secondary apertures, ×530. Fig. 26, *Deuterammina (Deuterammina) balkwilli* sp. nov. Holotype (N.M.I. no. 109.1981). Oblique view showing primary and secondary apertures, ×360. Fig. 27, *Paratrochammina (Paratrochammina) wrighti* sp. nov. Holotype (N.M.I. no. 110.1981). Oblique view of umbilicus and aperture, ×350. Figs 28–30, *Deuterammina (Centrodeuterammina) dublinensis* sp. nov. Holotype (N.M.I. no. 111.1981). Fig. 28, edge view of primary aperture, ×950. Fig. 29, oblique view of primary and secondary apertures, ×375. Fig. 30, oblique close-up view of secondary apertures within open umbilicus, ×1000.

plate does not cover the umbilical depression as it does in *Paratrochammina (Portatrochammina).* Murray's 1971 illustrations (pl. 17, figs 1–4 only) of *T. rotaliformis* could belong to this form.

Acknowledgements

We are extremely grateful to Dr Colin Harris (Trinity College, Dublin) who first brought the whereabouts of the Joseph Wright Collection to our attention. The Director of the National Museum of Ireland kindly allowed us to borrow the material and gave permission for Scanning Electron Microscopy. Mr Mark Holmes, Natural History Division, N.M.I., facilitated the loan. Mr R. V. Melville, International Commission of Zoological Nomenclature, once again advised us on taxonomic procedure. Drs C. G. Adams and L. R. M. Cocks, British Museum (Natural History) commented helpfully on the text. The work of P. Brönnimann is in part funded by the Fonds National Suisse.

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Notes on Atlantic and other Asteroidea. 3. The families Ganeriidae and Asterinidae, with description of a new asterinid genus

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Introduction

Examination of new and old material of these two closely related starfish families has prompted some additional observations on their limits and relationships, with consequent modifications to the diagnoses. A notable addition in the Ganeriidae is the abyssal genus *Vemaster* Bernasconi, 1965, formerly assigned to the Goniasteridae, but now shown by dissection of new specimens to be more closely related to *Ganeria,* a move supported by Downey and Blake (pers. comms). Several of the nominal genera proposed by Verrill (1913) for the Asterinidae are reevaluated, resulting in the synonymy of *Patiria* with *Asterina* and, conversely, in the revival of *Callopatiria.* Some recently collected asterinids from the Atlantic coast of Panama proved to represent a new genus remarkable for having many of the abactinal plates paxilliform.

A difficulty arose in formally citing the type species of *Asterina* itself, for which a possible solution to the nomenclatural problem is given in an appendix.

Systematic account

Families *GANERIIDAE* Sladen and *ASTERINIDAE* Gray

Blake (1981) has reviewed the history of these two families which he transferred to the order Valvatida from the Spinulosida. Briefly, Gray (1847) originally included *Ganeria* itself in his Asterinidae, being followed in this by Perrier (1875) and Viguier (1878). However, Sladen (1889) distinguished the subfamily Ganeriinae within the Asterinidae, on the basis of enlarged marginal plates, for *Ganeria* and *Cycethra* Bell, 1881 and this was raised to family rank by Perrier (1894). Later authors, notably Fisher (1911*a*) and Blake (1981), have emphasized the close affinity between the Ganeriidae and the Asterinidae. Fisher followed Sladen in distinguishing them on the basis of large size of the marginal plates in ganeriids but this does not take account of those individuals of *Cycethra* and all the species of the later-added *Perknaster* in which the marginals are reduced and the series may be barely, if at all, distinguishable over part of their extent. Bernasconi (1964) and Blake (1981) have separated them on the form of the abactinal plates, with well defined columns of various height in the Ganeriidae but with ridge-like elevations or gently rounded convexities in the Asterinidae (though Blake termed both plate forms 'metapaxilliform' since the basal part of each plate is variously enlarged and the elevation often excentric) but this again does not take into account the amazing variations of *Cycethra,* some individuals of which have simply convex or crescentic elevations indistinguishable from those of certain Asterinidae instead of the usual well-defined but low columns ranging from circular through oval to crescentic in section. Blake also utilized the arrangement of these plates, said to be in ill-defined rows in Ganeriidae but well-defined ones in Asterinidae; however, some asterinids, especially those of large size comparable to that of many specimens of *Ganeria* and *Cycethra,* have an essentially alternating abactinal skeleton, though alternate plates may have a secondarily longitudinal alignment, for instance in *Patiria granifera* (Fig. 6, below) and *Nepanthia crassa.*

In an attempt to assess the relationships of the various plate systems of Atlantic asteroids,

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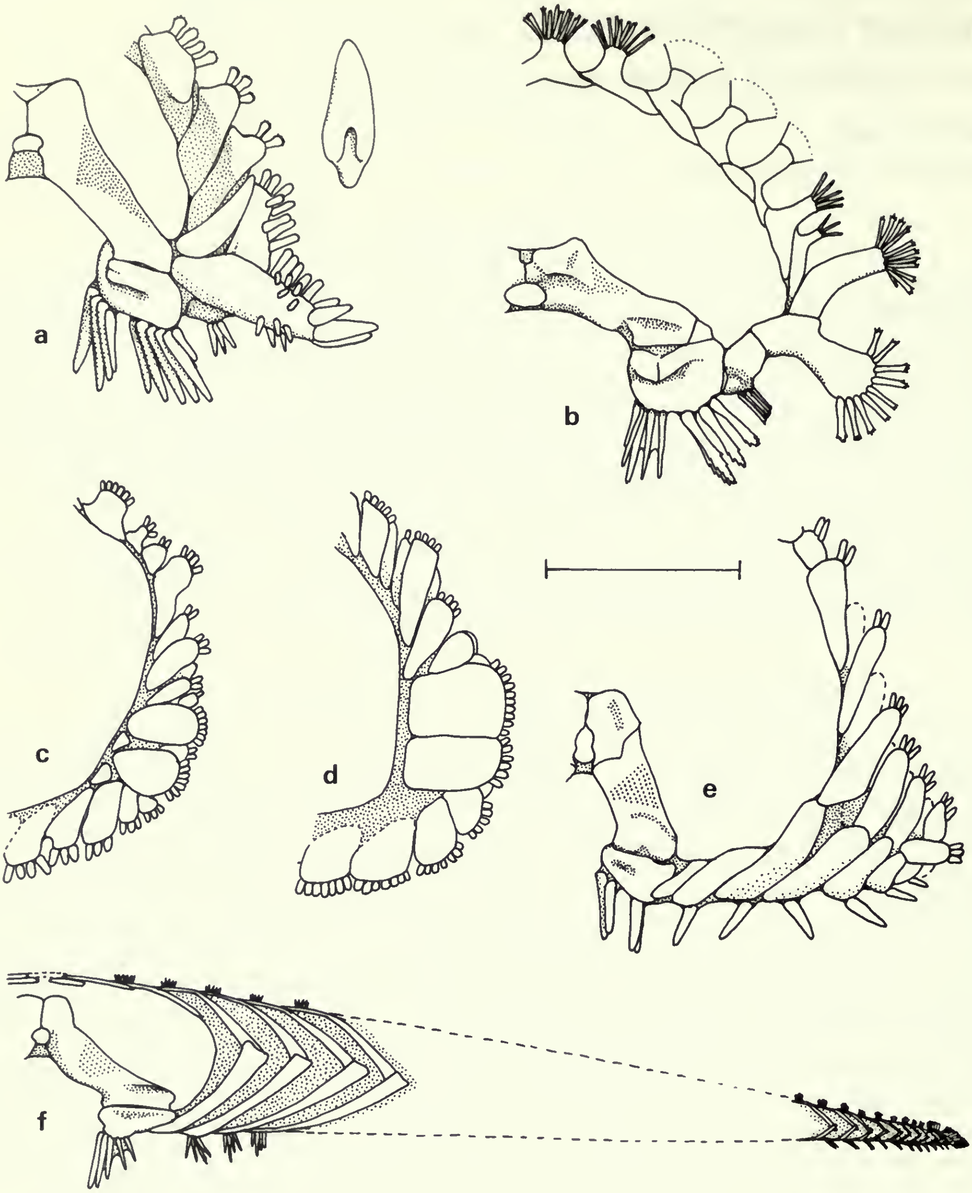

Fig. 1 Partial cross sections near base of ray viewed from proximal side of : (a) *Leilaster radians* (Perrier), *Gerda* st. 1270. Yucatan Channel, W of Cuba, 318 m, R 11·5–14·5 mm (with isolated inferomarginal plate viewed from above); (b) *Lophaster furcifer* (Düben & Koren), BM reg. no. 91.5.20.1, Trondheim fjord, R 30 mm; (c) *Cycethra verrucosa* (Philippi), 1971.9.1.4, N Argentina, R 40 mm; (d) *C. verrucosa,* formerly named *Patiria obesa,* 1948.3.16.356, mid-Argentina, R 33 mm; (e) *Asterina gibbosa* (Pennant), 98.5.3.171, Falmouth, Cornwall, R 15·5 mm; (f) *Anseropoda placenta* (Pennant), 88.10.8.1, W of Scotland, R 31–40 mm (oblique section following the lines of abactinal and actinal plates). Plates not in the plane of the section shown by discontinuous lines except in (f). The scale measures 2 mm for (a), 2·5 mm for (e) and (f), 3 mm for (b)–(d).

I have made cross-sections of the rays of some taxa. Where the Ganeriidae and Asterinidae are concerned, these do show considerable resemblances between some species of both families but I find there is always a more or less well-defined ventro-lateral angle at the level of the inferomarginal plates in the Asterinidae, whereas in ganeriids the contour of the ray in this area is curved, the actinal surface being slightly convex and merging into the side of the ray. Inevitably, in asterinids such as *Nepanthia,* where the well-defined arms are nearly cylindrical, the angle is least, but it is still distinct. Coupled with the superficial shape, the marginals of the Ganeriidae, when enlarged, are block-like, these of the two series similar in form and not wedged in by internal extensions of the lateralmost abactinal and actinal plates. In the Asterinidae the marginals of the two series are consistently small and often only recognizable by their regularity along the angle (the superomarginals sometimes barely distinct), the flattened inferomarginals appearing pearshaped or pegshaped in the sectional view and wedged in by the inner ends of the adjacent plates or some supernumerary internal plates which form a series of buttresses or a more continuous structure reinforcing the ventro-lateral angle (see Fig. 1e, 5b, c). In the extremely flattened asterinid *Anseropoda* the ventro-lateral angle is very narrow and the reinforcement for the upper side spans almost the entire body cavity of the ray, except for a narrow midradial area, taking the form of angled struts in obliquely transverse series, each made up by a slender flattened process from an abactinal plate overlapping the upper end of a similar process from the corresponding actinal plate (Fig. 1f).

One consequence of this study is realization that **Leilaster** A. H. Clark, 1938 is not a ganeriid. When established by Clark for type species *Korethraster radians* Perrier, 1881, from the Caribbean, Fisher evidently supported a proposal to include it in the Ganeriidae. He reiterated this in 1940 (pp. 152–153) when discussing the antarctic *Mirastrella,* which he referred to the Asterinidae though commenting that the 'produced inferomarginals' also suggested affinity with the Ganeriidae. Presumably he could then only have had *Leilaster* in mind, not the true ganeriids. A cross-section of a ray of the small *Leilaster radians* (Fig. 1a), where R is up to only *c.* 15 mm, shows a flat underside formed mainly by the relatively large cigarshaped inferomarginal plates which abut directly on to the outer ends of the ambulacral plates (the single actinal plate in a proximal section being superimposed). As viewed from above, the inferomarginals are slippershaped, tapering outwardly, and have a notch on the inner (adradial) half forming a socket into which fits the lower end of the vertically aligned corresponding superomarginal plate. The coarse abactinal plates imbricate adradially (the more lateral ones) or proximally (the midradial ones) and each is raised into a ridge or rounded column and crowned with coarse capitate spinelets. The formation of a lateral flange to the body made by the inferomarginal plates and the imbricating abactinals are characters shared with most asterinids but in *Leilaster* the inferomarginals are relatively much larger and nothing like their articulation with the superomarginals is shown in the asterinids studied, nor do they directly contact the ambulacral plates in asterinids without multiple series of intervening actinal plates—even at this relatively small size. Further, in *Leilaster* the proximal articulating face of the adambulacrals (which provides characters given considerable weight by Blake) is rectangular and has a complex near-horizontal groove unlike any of the squarish, slightly hollowed adambulacrals of the asterinids and other Valvatida studied.

These internal structures have yet to be studied in *Mirastrella biradialis* Fisher when more material is available. Consultation with Miss M. E. Downey of the Smithsonian Institution, co-author of the review of Atlantic Asteroidea for which the present note is a preliminary, yielded her opinion that *Leilaster* and *Mirastrella* are closely related. They share two unusual characters not shown by any ganeriids or asterinids. For one thing, there is a distinct groove (or fasciole) in each interradius running vertically from the margin up to the flat top of the disc between the two first superomarginals and the interradial abactinal plates above. Secondly, there are two longitudinal (but bowed) series of enlarged abactinal plates (the 'first adradial' series of Fisher) on each ray framing the three (*Leilaster*) or two (*Mirastrella*) longitudinal series of midradial plates like the two prongs of a wishbone.

The complex articulating face of the adambulacrals in *Leilaster* shows some resemblance to that of the spinulosan *Lophaster furcifer* (Düben & Koren) of the family Solasteridae (Fig. 1b). *Lophaster* also has reduced actinal areas, though the section made shows one actinal interposed between the inferomarginal and the ambulacral/adambulacral articulation, at least in the proximal part of a ray at R *c*.30 mm. The superomarginal in *Lophaster* has a tall paxillar column and a triradiate base, two lobes of which articulate with the upper side of the expanded adradial part of the inferomarginal straddling a median hollow which does not form a socket. The marginals as well as the abactinal plates in *Lophaster* and other solasterids are highly paxilliform with slender rounded columns, rather than being metapaxilliform as in *Leilaster.* Even so, I think Verrill (1915) had some justification for treating a specimen with R 35 mm, three times that of the type of *L. radians,* as conspecific; his specimen was renamed *Lophaster verrilli* by A. H. Clark in 1938. Whether or not the small specimens which have been referred to *Leilaster radians* and *Mirastrella biradialis* should be referred to the Spinulosida remains to be determined from a review of that order.

Another genus of uncertain affinities is the diminutive abyssal **Vemaster** Bernasconi, 1965, from the Argentine Basin (maximum R only 15 mm). Because of some resemblance in the tabulate abactinal plates to *Cladaster* and *Nectria* Bernasconi referred *Vemaster* to the Goniasteridae. However, examination of some additional material of *Vemaster* shows that the superomarginal plates are undeveloped and the inferomarginals displaced to a ventrolateral position and not at all blocklike (both marginal series being essentially well-developed and blocklike in Goniasteridae), there is no regularity in the arrangement of the abactinal plates and the actinal plates are very reduced and irregular, being possibly secondary calcifications. Also, internally *Vemaster* has an archlike calcified interbrachial column arising from near the oral plates in each interradius, curving laterally at its upper end to meet the lateral wall of the disc, this compares with a solid calcified interbrachial buttress fused to the side of the disc in *Nectria,* which genus also has superambulacral plates developed (according to Fisher, 1911*a*), not observed in *Vemaster*, besides having regularly arranged abactinals. However, just such an inclined columnar interbrachial support is found in Ganeriidae such as *Cycethra* and *Perknaster* (indeed in the specimen of *P. sladeni* studied, this structure is arched over as in *Vemaster*), which genera also show a marked tendency for reduction of the marginals and loss of their blocklike form, especially *Perknaster*, where the abactinal plates are irregular and the actinal areas somewhat reduced.

Apart from the much finer abactinal skeleton of *Perknaster,* the main difference between it, together with the other southern genera of Ganeriidae, and *Vemaster* is the absence of a ventrolateral angle—emphasized above as a characteristic feature of the family in comparison with the Asterinidae—whereas the inferomarginals of *Vemaster* form a distinct projection in this area, the arms being D-shaped in cross-section with the ventral side quite flat. The asterinid *Nepanthia* does have an almost D-shaped arm section but here actinal plates are developed in regular series on the arms and superomarginals combine with the inferomarginals to make the ventrolateral angle.

Both Downey and Blake (pers. comms) support reference of *Vemaster* to the Ganeriidae. However, in view of the marked difference in arm section, I think that its isolation in a separate subfamily from the closely related *Ganeria, Cycethra* and *Perknaster* may prove to be desirable. This problem must await comparison of all these with other genera from parts of the world outside the Atlantic which have been referred to the Ganeriidae but which seem to me less closely interrelated than are the three Southern Ocean genera. These other genera are: *Aleutiaster* A. H. Clark, 1939, from the Aleutian Is, North Pacific, *Hyalinothrix* Fisher, 1911b, from the Hawaiian Is, *Knightaster* H. E. S. Clark, 1972, from New Zealand and *Tarachaster* Fisher, 1913, from the Philippines with a second species from New Zealand of McKnight, 1973, the rest being monotypic.

Another taxon which the study of arm sections shows to have been misplaced is **Patiria** (originally *Parasterina*) **obesa** (H. L. Clark, 1910), recorded from both sides of southern South America. In 1962 I renamed as *P. obesa* four *Discovery* specimens from southern Argentina (which Fisher (1940) had identified as *Cycethra verrucosa* forma *nitida*) since they

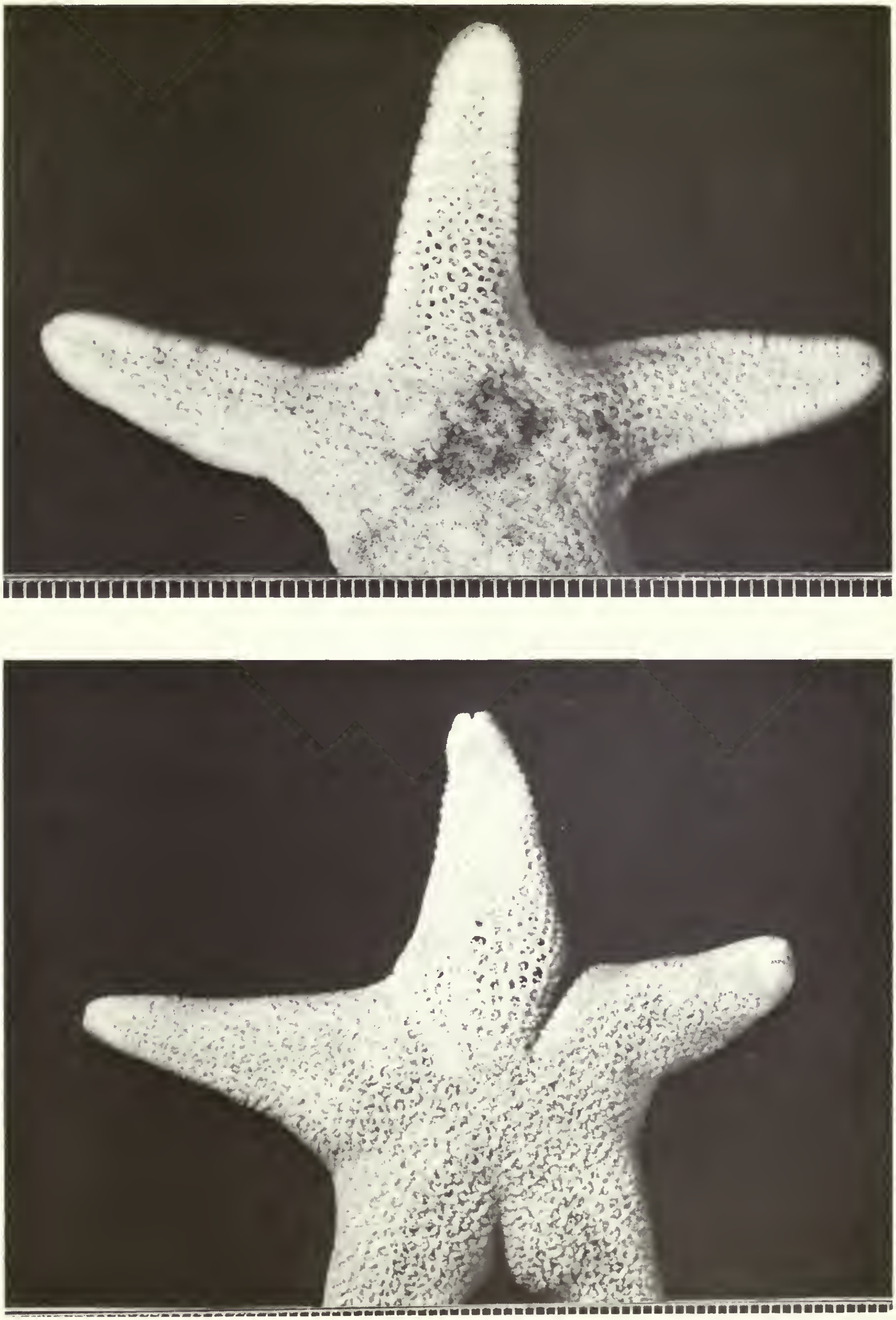

Fig. 2 *Cycethra verrucosa* (Philippi), BM reg. no. 1948.3.16.356, Argentina, R 33 mm (formerly named *Patiria obesa*), ×2 (above) and 1948.3.16.344, W Falkland I, R 39 mm, with more abrupt elevations on the abactinal plates but reduced marginals, $\times 1\frac{1}{2}$ (below).

closely resemble the photographs of H. L. Clark and of Madsen (1956) of *P. obesa* from Chile and have notably asterinid-like abactinal plates with only low crescentic convexities, though some of them have the distal superomarginals enlarged in an 'un-asterinid-like' way (fig. 2 top). Madsen also recorded an Argentinian specimen as *obesa* and noted that the development of the marginals varies from barely distinct (as in the holotype) to fairly conspicuous, as in the *Discovery* specimen sectioned (Fig. 1d) and even more the one photographed. These marginals are block-like and those of the two series similar in shape, forming a curved surface with no sign of an angle at the inferomarginal. Bernasconi too (1973) found the marginal area of *obesa* to be thick and rounded. Such a form matches that of some specimens of *Cycethra verrucosa,* in which species the marginals show a similar wide range of development, whereas in asterinids the marginals variously developed have been found to have the abactinal plates variously developed with elevations ranging from ill-defined columns to crescentic rounded convexities. I must therefore concede the correctness of Fisher's identification of the *Discovery* specimens, from which it follows that *Patiria obesa* is yet another synonym of *Cycethra verrucosa* (Philippi, 1857), a taxon so variable that I think it futile to try and treat *Cycethra* as other than a monotypic genus.

Madsen and Bernasconi both compared *P. obesa* with *P. bellula* Sladen of South Africa, the type species of *Callopatiria* Verrill, 1913, synonymized with *Patiria* by Fisher (1940); Madsen suggested 'perhaps this genus [*Callopatiria*] ought to be retained and also include the species *obesa*', an idea supported by Tortonese (pers. comm.). I too agree that *Callopatiria* deserves recognition, as discussed below, and think it comes closest of all the asterinids to *obesa,* though I am convinced that the true place of *obesa* is among the Ganeriidae.

In his drastic summary revision of the Asterininae (1913), Verrill recognized no less than 12 nominal genera in addition to *Stegnaster* and *Tremaster,* since isolated in a separate subfamily, four of them unconnected with the Atlantic fauna, leaving the following for consideration:

Asterina Nardo, 1834. Type species (see appendix, p. 378): '*Asterias minuta*=*A. gibbosa* (Pennant, 1777)' by subsequent designation by Fisher, 1906.
Asterinides Verrill, 1913. Type species: *Asteriscus folium* Lütken, 1860.
Patiria Gray, 1840. Type species: *P. coccinea* Gray, 1840, a synonym of *Asterias miniata* Brandt, 1835.
Patiriella Verrill, 1913. Type species: *Asterina regularis* Verrill, 1867.
Asterinopsis Verrill, 1913. Type species: *Asterias penicillatus* Lamarck, 1816.
Enoplopatiria Verrill, 1913. Type species: *Asteriscus marginatus* Hupé, 1857, a nom. nud. conspecific with *A. stellifer* Möbius, 1859.
Callopatiria Verrill, 1913. Type species: *Patiria bellula* Sladen, 1889, a synonym of *P. granifera* Gray, 1847.
Allopatiria Verrill, 1913. Type species: *P. ocellifera* Gray, 1847.

Of these, **Asterinides** has been synonymized with *Asterina* by Fisher (1919), in his Philippine book, on the grounds that the absence of pedicellariae (the only distinction given by Verrill) is not a character of generic weight. However, Brito (1968) apparently overlooked this and Tommasi (1970) disregarded it, both of them retaining *Asterinides* for *folium* without further justification. Although occurrence of pedicellariae is unreliable even as a specific character, the name *Asterinides* might be utilized, at least at the subgeneric level, for a group of species with the body relatively low and near pentagonal (though this alone is not of supraspecific weight) correlated with very fine, easily detached abactinal spinelets. Besides *A. folium* it could also include the Indo-Pacific *sarasini* group of species discussed in Clark & Rowe (1971 : 67–68).

Verrill (1913; 1914*a* & *b*) differentiated his nominal genera only in two versions of a dichotomous key, the 1913 one confused by the omission of one option: DD. 'Interactinal plates without a fan of spines', which I think should have come on p. 480 after *Enoplopatiria* and been immediately followed by b and bb (for *Patiriella* and *Asterinopsis*) though Verrill

(1914*a*) proposed its insertion on p. 479 after EE and before x for *Patiria* which *does* have fans of spines on the actinal plates. It appears that *Enoplopatiria,* resulting from xx, must have been an afterthought, since the sequence in the key is otherwise alphabetical from A to G. The 1914*b* version shows Verrill's true intention and this was clarified by Fisher (1919), who adopted *Patiriella* and produced a simplified key to the Pacific genera of Asterininae, differentiating **Patiriella** and **Patiria** from **Asterina** by the abactinal structure, simpler in *Asterina* with the plates of the papular areas of only one kind and rounded, elliptical, cordate or shieldshaped (in Verrill's words), as opposed to plates of two or more diverse kinds, the larger arched or crescentic and notched for the papulae and the smaller ones ovate or pear-shaped and inserted endwise (vertical to the surface) between the larger.

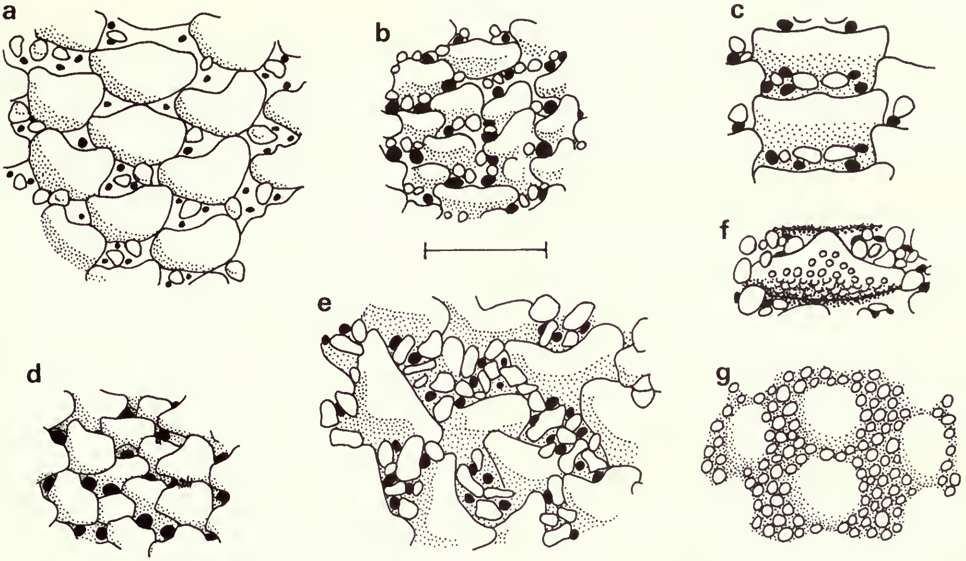

Fig. 3 Denuded abactinal plates from proximal part of midradial area of: (a) *Asterina gibbosa* (Pennant), BM reg. no. 1960.8.4.4, Syra, Aegean Sea, R 27 mm; (b) *Asterina* (formerly *Patiria*) *miniata* (Brandt), 1954.9.8.43, San Pedro, S California, R 16 mm; (c) *Patiriella regularis* (Verrill), 1970.10.8.111, Nelson, New Zealand, R 21 mm; (d) *Asterina folium* (Lütken), USNM no. 38811, Sand Key Reef, S Florida, R 8 mm (a few surviving spinelets shown at the proximal ends of two plates); (e) *Callopatiria* (formerly *Patiria*) *granifera* (Gray), 1903.8.1.47, Mossel Bay, S Africa, R 40 mm; (f) *Asterina* (formerly *Patiria*) *stellifera* (Möbius), 1936.10.14.3, Accra, Ghana, R 41 mm; (g) *Allopatiria ocellifera* (Gray), 1969.12.16.13, Cape Lever, Mauritania, R 38 mm. The scale measures 4 mm for (g) and 2 mm for the rest; (a) and(f) are from wet specimens, the pores appearing relatively small.

However, examination of a relatively large specimen of *Asterina gibbosa* (R 27 mm) (Figs 3a, 4 top) shows closer agreement of the abactinal skeleton with the second option than the first, there being two or even three small secondary plates in some of the papular areas and the primaries in the papular areas *are* mostly crescentic. The type species of both *Patiria* and *Patiriella* reach a considerably larger size, $R > 60$ mm, and develop many more secondary plates though at $R < 30$ mm these are relatively few in number (Fig. 3b, c). The form and arrangement of the other plates, including the internal ones buttressing the lateral angles of the arms (see Fig. 1e), and the armament of *A. gibbosa* and the other two type species, do not seem to me significantly different, while the difference in maximum size alone seems inadequate for the distinction of genera. Verrill's keys tried to distinguish *Patiriella* from *Asterina* also by the reduced actinal armament of usually only a single spine, rarely more

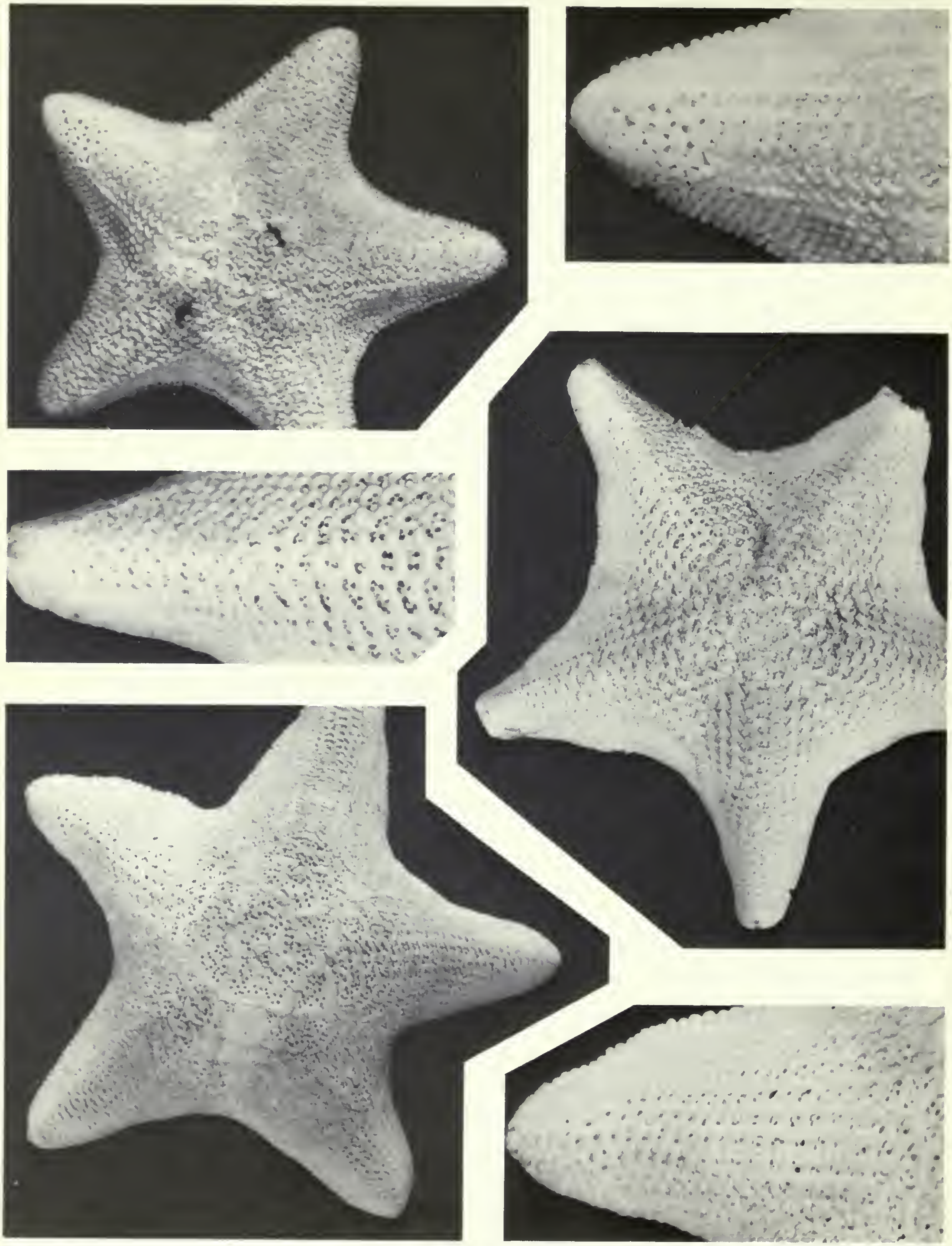

Fig. 4 Dorsal views, ×1½, and enlargements of denuded rays, ×3, of: *Asterina gibbosa* (Pennant), BM reg. no. 1960.8.4.4, Syra, Aegean Sea, R 27 mm (above); *Asterina* (formerly *Patiria*) *miniata* (Brandt), 1954.9.8.43, San Pedro, California, R *c.*32 mm (middle); *Patiriella regularis* (Verrill), 1970.10.8.112, Golden Bay, New Zealand, R 30 mm (below).

than two on a plate. Dartnall (1971) in diagnosing *Patiriella* also noted that the abactinal armament is short, granular and bluntly capitate, the carinal (midradial) plates are doubly notched to accommodate two longitudinal rows of papulae and pedicellariae are lacking. The other characters he mentioned are common to *Asterina gibbosa* and indeed some of the midradial plates in that species also subtend two pores though the three proximal lobes are less marked than in *Patiriella regularis.* Small specimens of *A. gibbosa* and many *A. burtoni* Gray, for instance, also have no more than two actinal spines. However, the particularly coarse and abbreviated abactinal armament in the australasian species *P. regularis* and *P. gunni* (Gray), as well as the pan-oceanic *P. exigua* (Lamarck), and perhaps the frequent development in these of a regular pair of secondary plates proximal to some of the trilobed midradial primaries (not observed in *A. gibbosa*), may serve to justify retention of *Patiriella* with generic (or perhaps subgeneric) rank. Dartnall (pers. comm.) shares my doubts about the generic distinction of *Patiriella.* Since Australia is rich in species of both *Patiriella* and *Asterina,* the resolving of this problem seems best left to one of the several interested Australian specialists, the name *Patiriella* being retained here for *P. exigua* which extends to St Helena.

Patiria miniata from the NE Pacific was only shown to be the type species of *Patiria* in 1933 when Mortensen synonymized with it *P. coccinea* Gray, mistakenly recorded from South Africa. Fisher (1911*a*), in his N Pacific asteroid monograph, had included *miniata* in *Asterina* and this combination has been perpetuated in the Pacific literature for both *miniata* and the closely related Japanese *pectinifera* (Müller & Troschel). These two differ from *Asterina gibbosa* (apart from the greater maximum size) in lacking pedicellariae but this is not true of *P. stellifera* (Möbius), the type species of **Enoplopatiria,** from E South America and W Africa, which is otherwise very similar to *P. miniata* in shape, plate structure and armament. *Enoplopatiria* was synonymized with *Patiria* by Fisher (1919), discounting the taxonomic weight of the occurrence of pedicellariae, as with *Asterinides,* but *Enoplopatiria* was similarly retained by some South American authors, in this case Bernasconi (1955), as well as Brito (1968) and Tommasi (1970). However, Madsen (1950) had used *Asterina* for *stellifera* and this was followed by me in 1955. Subsequently I expressed doubts (quoted by Tommasi) about this position for *stellifera* because of the many secondary abactinal plates and, in Clark & Courtman-Stock (1976), like Tortonese (1956) and Bernasconi (1966), used *Patiria stellifera.* I am now forced to the reverse, rejecting greater maximum size and its commensurate elaboration of the abactinal skeleton as justifying a generic distinction; both *Enoplopatiria* and *Patiria* itself are therefore to be synonymized with *Asterina.*

Of the remaining species currently included in *Patiria, P. obesa* (H. L. Clark, 1910) is referred above to the synonymy of *Cycethra verrucosa, P. granulosa* (Perrier, 1875), supposedly from the Hawaiian Is, was based on specimens which appear to be conspecific with *P. miniata* (indeed, one sample is so referred in the catalogue of the Paris Museum collections) and *P. chilensis* (Lütken, 1859) is also close to *miniata* and so falls within *Asterina.* This leaves only *P. granifera* Gray, 1847 and *P. formosa* (Mortensen, 1933), both from South Africa, *P. obtusa* Gray, 1847, supposedly from Pacific Panama and *P. pulla* and *P. rosea* both of Koehler & Vaney, 1906, from Mauritania, these last two dealt with below under *Allopatiria.*

Patiria granifera is type species (by synonymy with *C. bellula*) of **Callopatiria,** which was formally synonymized with *Patiria* by Fisher in 1941, since Mortensen (1933) cited *C. bellula* in the references to [*Parasterina*] *bellula* and Fisher himself (1940) returned *bellula* to *Patiria.* In 1956 I synonymized *bellula* with *granifera.* Comparison of arm sections of this species with *Patiria* (or *Asterina*) *miniata* now shows a significant difference in the alignment of the superomarginal plates, those of *P. granifera* and the closely related *P. formosa* having both superomarginal and inferomarginal plates projecting to a similar degree together forming the ventrolateral angle (Fig. 5b)—whereas in *Asterina* sensu lato, *Patiriella* and *Allopatiria,* the angle is sharper and formed only by the inferomarginal series projecting beyond the inset superomarginals which may be hardly distinguished from the adjacent abactinal plates and can alternate in position with the inferomarginals along the arm. Of

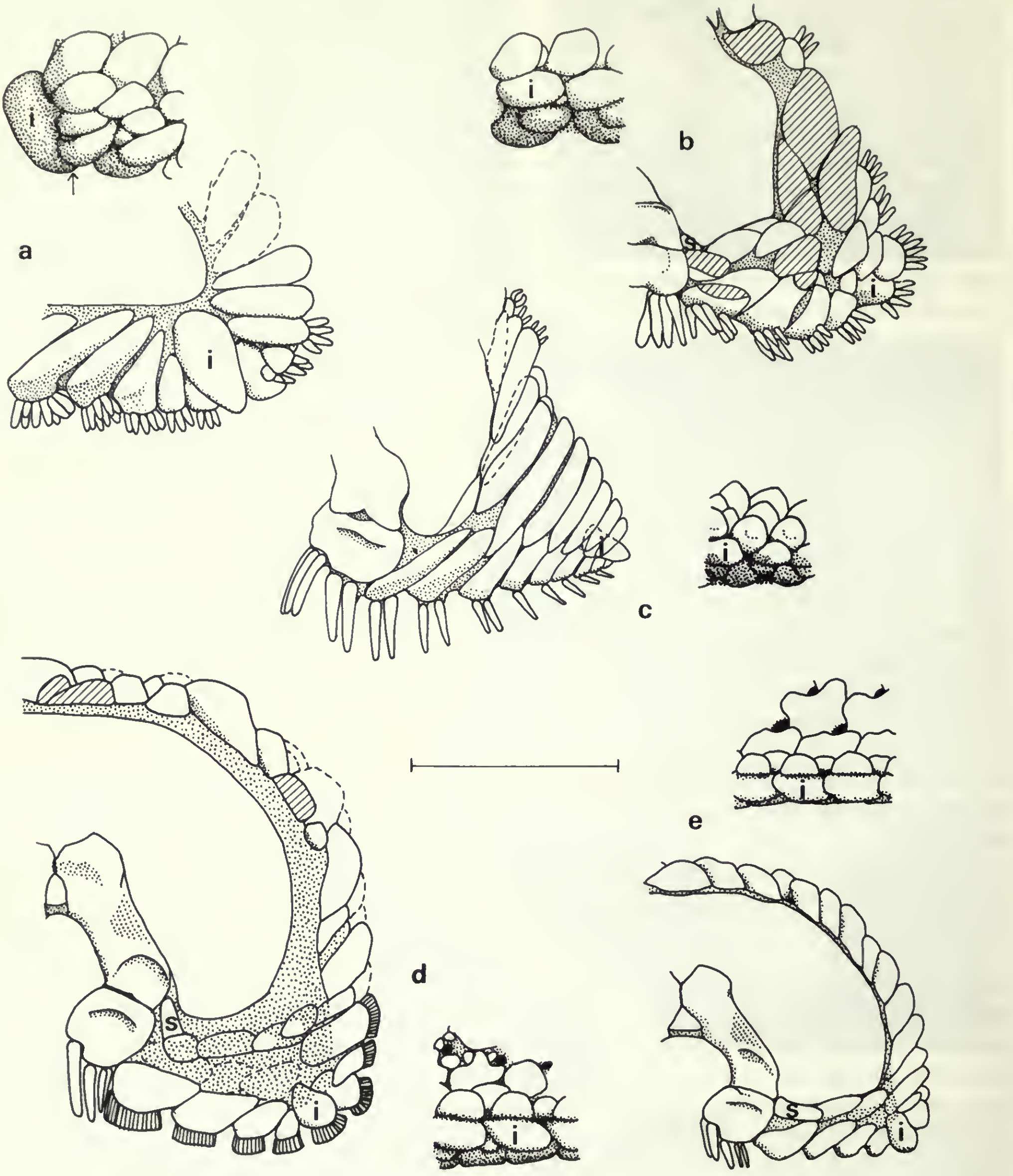

Fig. 5 Partial cross sections near base of ray viewed from proximal side, with lateral views of marginal area immediately distal to section, of: (a) *'Patiria' obtusa* Gray, holotype, BM reg. no. 1938.6.23.24, Panama, R up to 54 mm (the arrow shows the plane of the section where the internal part of the inferomarginal is exposed); (b) *Callopatiria* (formerly *Patiria*) *granifera* (Gray), 81.6.22.14, Cape Town, R 29 mm; (c) *Asterina* (formerly *Patiria*) *stellifera* (Möbius), USNM, Angola, R *c*.35 mm; (d) *Nepanthia crassa* (Gray), 61.7.8.32, Fremantle, Western Australia, R 40 mm; (e) *N. brevis* (Perrier), 81.10.26.172, Albany I, N Australia, R 28 mm. The parallel rows of dots on the ambulacral plates show the hyaline areas over which the tube foot slides; hatching shows cut surfaces of plates and discontinuous lines indicate plates not in the plane of the section; in (d) the outlines of the plates buried in the body wall are hypothetical. The scale measures 3 mm.

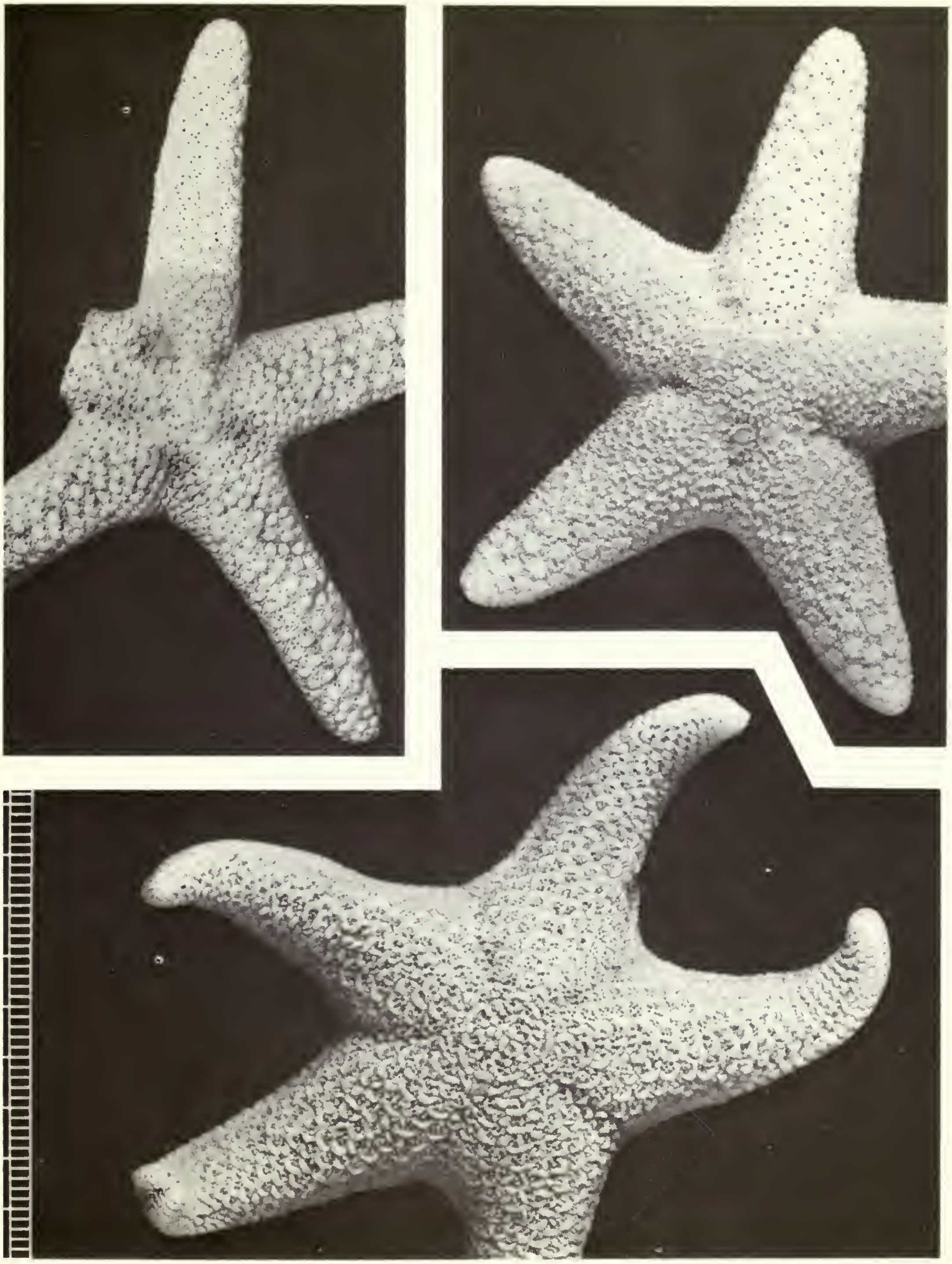

Fig. 6 *Nepanthia crassa* (Gray), BM reg. no. 61.7.8.32, Fremantle, Western Australia, R *c.* 38 mm (above left); *Callopatiria* (formerly *Patiria*) *formosa* (Mortensen), 1975.10.29.62, False Bay, South Africa, R 36 mm (above right); *Callopatiria* (formerly *Patiria*) *granifera* (Gray), 1948.3.16.798, Saldanha Beach, South Africa, R 45 mm (below). All ×1½.

the Asterininae studied, only in the Indo-Pacific **Nepanthia** does the marginal structure approximate to that in *P. granifera* and *formosa,* the sides of the ray being approximately vertical and the angle rounded, especially in species such as *N. belcheri* (Perrier) with thicker body walls and more numerous secondary abactinal plates.

Several other differences mark off *P. granifera* and *formosa,* together with *Nepanthia,* from the rest of the Asterininae under discussion. Firstly, the primary abactinal plates along the midradial line in the former are all crescentic or rounded and have an alternating or irregular arrangement whereas in larger specimens of *Asterina gibbosa* and other Asterininae some of these plates are proximally trilobed and tend to form at least a partial single longitudinal row, though this may be double for some of its length (Figs 3a–c, f). Secondly, some of the secondary abactinal plates are elongated in the superficial plane instead of vertical to it in the South African species and the *Nepanthia* species where such plates are numerous. Lastly, and perhaps most importantly, the transverse sections show that there are internal ventral plates bracing the ambulacrals by linking them with the actinals and other additional plates integrated with the ventrolateral angle, the adradialmost of which are equivalent to superambulacral plates. In *Nepanthia brevis* (at least in the holotype) the superambulacrals are fairly regular in size and position and, in the proximal part of the arm at least, link through two other internal plates overlying the actinals to the lateral bodywall (Fig. 5e). However, in the specimen of *Patiria granifera* sectioned, these plates are less well developed and not regularly aligned, being also partly immersed in the fleshy internal part of the ventral bodywall (Fig. 5b). In *Nepanthia crassa* (formerly *Parasterina* but provisionally referred to *Nepanthia* by Fisher (1941) and confirmed there by Rowe & Marsh, 1982) there is massive ventral thickening of the body wall reinforced with irregular plates, some acting as superambulacrals, more or less deeply embedded in the soft tissue (Fig. 5d). *N. crassa* also carries to an extreme for *Nepanthia* the number of secondary (and even tertiary) abactinal plates. At the same time, its primary abactinals develop a more rounded than crescentic form compared with other *Nepanthia* species such as *N. belcheri,* such a modification having a parallel in *P. formosa* as opposed to the *P. granifera* (and indeed in *Allopatiria ocellifera* as opposed to the geographically adjacent *Asterina stellifera*). Marsh (pers. comm.) confirms the presence of obscured superambulacrals in *N. crassa* and has also found them in *N. maculata* and *belcheri.* This structure contrasts with the other Asterininae where the reinforcing plates for the ventrolateral angle do not extend adradially to help support the ambulacral arch (see Figs 1e, 5c). Blake (pers. comm.) suggests that the development of superambulacrals in this instance is correlated with the relatively narrow and more nearly cylindrical arms, compared with most asterinids. The two South African species approximate to *Nepanthia* in body form, though the arms broaden slightly at the base to make blunt-angled or rounded interradial arcs.

Clearly, if these characters are as important as I believe (particularly the last), then the affinities of *P. granifera* and *formosa* are with *Nepanthia* (and especially with species such as *N. crassa* and *N. belcheri* with thicker body-walls and more numerous secondary abactinal plates) rather than with *Patiria* sensu Gray, 1840—now synonymized with *Asterina.* However, this contradicts Fisher's conclusion of 1941 that *granifera* is close to *Patiria miniata* but *crassa* is allied with *Nepanthia.* If Fisher's evaluation of the affinities is correct and at least a generic distinction should be recognized between *granifera* and *crassa,* then *Callopatiria* needs to be revived for *P. granifera* and *formosa.* The zoogeographical separation, with the westernmost record for *Nepanthia* being from Burma, supports such a distinction but the morphological characters are individually relatively unimportant. They include the following: In the two South African species the arms are less well defined basally so that the interradial arcs are rounded or only bluntly angled; the superomarginal plates appear to match the inferomarginals in size during growth, the successive ones remaining contiguous whereas in most Nepanthias seen the superomarginals are smaller, some of them being separated by interstitial abactinal plates and in *N. briareus,* which has particularly cylindrical arms and ill-defined ventrolateral angles, the superomarginals outnumber and fail to match the inferomarginals; the actinal armament is much more coarse while the spinelets

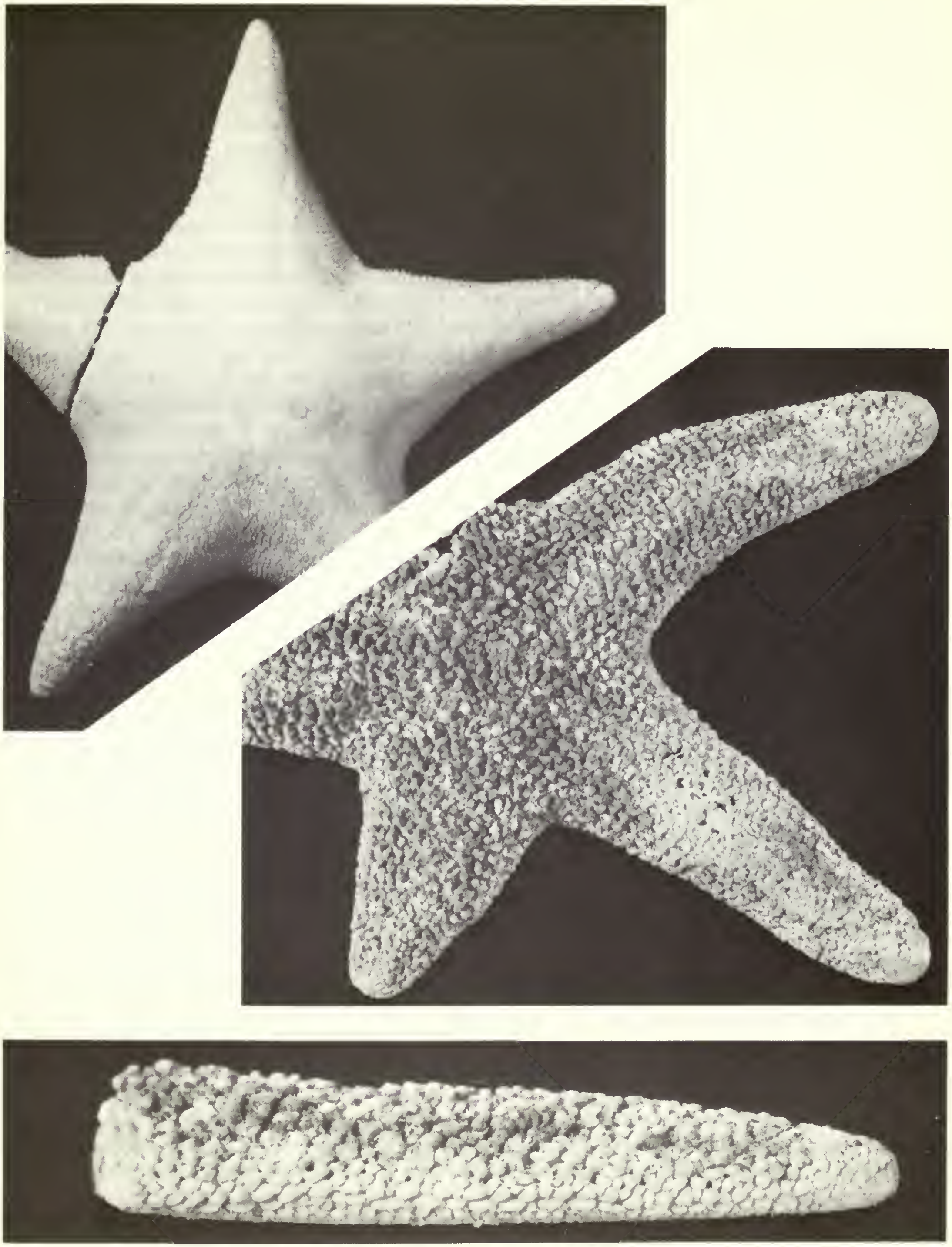

Fig. 7 *Allopatiria ocellifera* (Gray), BM reg. no. 1969.12.16.13, Cape Lever, Mauritania, R 38 mm (the uppermost ray denuded), × 1½ (above); *'Patiria' obtusa* Gray, holotype, 1938.6.23.24, Panama, R up to 54 mm (the lower right ray partly denuded, and a few plates lost) × 1½ (middle), side view of detached arm, partly denuded, of the same, × 3 (below).

of at least the proximal plates usually number less than ten and form single or double fans, especially in *formosa,* rather than being very fine and forming dense clusters as in the species of *Nepanthia*; lastly, the development of the superambulacral plates is less advanced, as outlined above. Cumulatively, these differences probably do justify the revival of *Callopatiria* with generic rank but the relationship with *Nepanthia* merits further attention. That genus has already been broadened in concept considerably by the inclusion of *Parasterina crassa* with its very thick body wall and complex abactinal skeletal structure.

The only remaining species of *Patiria* is *P. obtusa* Gray, 1847. The poorly preserved holotype ((Fig. 7 below) with its relatively long arms (R/r 53/17 mm = 3·1/1) and irregular abactinal plating (possibly at least partly due to the condition) appears very unlike an *Asterina* but superficially resembles *Callopatiria granifera,* with which Verrill (1913) considered it congeneric. However, the similarity does not extend to the internal characters since the broken arm shows a complete absence of any superambulacrals or other internal reinforcing plates. The inferomarginals are relatively large, appearing pearshaped in the section view (Fig. 5a) but flattened and tapering externally to appear long oval on the surface; their relatively ventral position is probably due to the unnatural flattening of the specimen and this may also account for the rounded ventro-lateral profile. The species is not a ganeriid since the marginals are not at all blocklike, the adjacent abactinal and actinal plates are strongly imbricating so as to reinforce the ventrolateral area, quite unlike those individuals of *Cycethra* with marginals reduced to this same small superficial size. Without more material in better condition, a proper assessment of the position of *'Patiria' obtusa* among the asterinids cannot be made. The species is known only from the holotype, Verrill's near-pentagonal specimen from Panama recorded under this name (1869) with its relatively sparse actinal armament (rather than dense clusters of spinelets) being some other asterinid (perhaps *Enoplopatiria siderea* Verrill, 1913, also from Panama). Neither H. L. Clark (1940) in the echinoderms of the *Zaca* expedition to west Central America, nor A. H. Clark (1946) in the echinoderms of the Pearl Islands, Bay of Panama, recorded *obtusa,* so there must be an element of doubt about its source.

The name **Asterinopsis** has been declared invalid by H. L. Clark (1938), since Mortensen (1933) noted that Lamarck's material of the type species is lost and its precise locality was uncertain. H. L. Clark noted that the two Atlantic species included in *Asterinopsis* by Verrill: *Asterina lymani* and *A. pilosa* of Perrier, 1881, are not congeneric with the Indo-Pacific species subsequently included, leaving them in limbo when he transferred some of the non-Atlantic species to *Paranepanthia* Fisher, 1917.

Finally, **Allopatiria** was for long of uncertain value, owing to ignorance of the type locality of the only species, *Patiria ocellifera* Gray, Verrill's supposition of Australia being unsubstantiated. In 1963 I redescribed the holotype, prompted by Professor Tortonese who had just discovered a similar specimen from the Mediterranean and who subsequently (1963) synonymized with *A. ocellifera* the Mauritanian *Parasterina africana* Engel & Croes, 1960. I believe that both *Patiria rosea* and *P. pulla* Koehler & Vaney, 1906, again from Mauritania, are also synonyms of *A. ocellifera.* Apart from colour differences in the type specimens (pink/red as opposed to grey with yellow spots) these two were supposed to differ from one another by minor differences in the body shape, the denuded condition of some of the enlarged abactinal plates in the holotype of *rosea* and different degrees of prominence of the furrow spines—the last two almost certainly due to artefacts of preservation. Madsen (1950) has already suggested that these differences are only individual variations when he provisionally synonymized *pulla* with *rosea.* The figures of *rosea* (1906, pl. 5, figs 3, 4) show a considerable resemblance to the holotype of *A. ocellifera* illustrated in A.M.C. (1963, pls 1, 4), despite the much larger size of the latter (R *c.*80 mm as opposed to 43 mm in the holotype of *rosea*).

Allopatiria ocellifera has a very distinctive abactinal skeleton with extremely numerous secondary plates (at least at R > 30 mm), many of them superimposed on the primary plates (or at least their peripheral parts), so that only rounded areas of most of the radial 'field' primaries of the rays are not overlain (Fig. 3g). The armament of the primaries (when intact) is a dense covering of short blunt spinelets, though the secondaries often bear a high proportion of two- or three-valved spiniform pedicellariae. *Asterina stellifera* also has similar pedicellariae, body form and large maximum size (R max. >50 mm) and occurs in West Africa to the south of Cape Verde, as well as on the east coast of South America. Despite these factors, I think that Verrill's generic distinction is well justified. *A. stellifera* and the other species of *Asterina* have short but broad midradial primary abactinals, many of them with a more or less well marked double concavity in the proximal side formed by three lobes of varying prominence and the other primaries of the pore areas are clearly crescentiform. A relatively small specimen of *Allopatiria ocellifera* (a paratype of *Parasterina africana*) with R 17 mm has three longitudinal series of apparently round primary plates on the radial 'fields', the more proximal ones revealed as rhombic when the spinelets are removed, the widest part being at the middle of the length. These plates just imbricate at the angles and the secondaries are limited to the interstitial rounded popular areas between them, numbering up to five in each area. The distal primaries, especially of the two outer series, become relatively broad and short and their armament resolves itself into two transverse linear series of spinelets. As growth proceeds, the secondaries become much more numerous, encircling the primaries and then encroaching progressively on their upper surface so that at R 80 mm (possibly before) only some of the distalmost primaries (which have become relatively large and rounded) are exposed except for their spinelets (A.M.C., 1963). This highly modified abactinal skeleton I believe fully justifies retention of a generic distinction for *Allopatiria* as suggested by Tortonese (1963).

Before revised diagnoses can be given of the families Ganeriidae and Asterinidae in the light of the present comments, it is necessary to describe a new aberrant genus of Asterinidae.

Genus *PAXILLASTERINA* nov.

DIAGNOSIS. A genus of Asterinidae with very flat, almost pentagonal, body form; primary abactinal plates not arranged in distinct radial and lateral 'fields' but regularly arranged, thin and flat except for an abrupt, short, flat-topped central column on many plates, including the midradial row of proximally 3-lobed plates, the columns replaced on others—especially the first adradial row each side of the midradial row—by a smaller rounded convexity, all these elevations crowned by a tall pompom or rounded tuft of numerous slender spinelets which are embedded in a soft matrix so as to radiate from a central conical core and not articulate directly with the elevation on the plate; only a few small secondary abactinal plates present proximally; margin very thin, formed by the inferomarginal plates only, the superomarginals small and inset dorsally; actinal and adambulacral plates armed with relatively few (<6) slender spinelets webbed together into fans; no pedicellariae observed.

TYPE SPECIES. *Paxillasterina pompom* sp. nov.

REMARKS. Superficially the small asterinid on which this new genus is based (R only *c.*15 mm in the four specimens) resembles the flatter, more nearly pentagonal species of *Asterina* such as *A. folium* (Lütken) but is marked off on closer scrutiny by the many paxilliform abactinal plates and their peculiar armament. It should be noted that in poorly-preserved and especially in dried specimens the pompoms contract and may become appressed on to the surface and the low paxillar columns can only be appreciated when the skeleton is denuded. Possibly similar specimens have been collected and attributed to the common Caribbean *A. folium,* this modification having been overlooked. It necessitates an alteration to the diagnosis of the Asterinidae in which truly paxilliform plates were not previously known. Conversely the diagnosis of the Ganeriidae also needs to be qualified to allow for the non--paxilliform plates of individuals of *Cycethra verrucosa* such as were previously referred to *Patiria obesa.*

Paxillasterina pompom sp. nov.
Figs 8, 9

HOLOTYPE. Korbiski Reef, San Blas Is, off Atlantic Panama east of the Canal Zone, *c*.6 m., under coral rubble. Collected by Dr G. Hendler.

R/r 14/11 mm = 1·3/1. The form is pentagonal, the body thin with central height only 5 mm (including the armament). The primary abactinal plates are very regularly arranged in rows parallel to the radii (or in chevrons if regarded interradially), and there is no distinction of radial and lateral 'fields' of plates, though the more adradial plates have the superficial part crescentic visible when denuded, subtending a single papular pore, except for the plates of the mid-radial row which have a median proximal lobe and a double concavity subtending two pores, the more lateral plates rhombic or fan-shaped; all these plates rather thin with only an inconspicuous texturing of crystal bodies and flat except for a central elevation which takes the form of a well-defined but low flat-topped column on many plates, including all of the midradial row and most of the second adradial each side, as well as scattered other plates; these columns crowned by a tall ovate pompom of numerous fine needle-like spinelets numbering up to *c*.50 and embedded in a soft matrix so that their bases arise from a central uncalcified cone and not directly from the column; other primary plates, including the first adradial row, have a small rounded central convexity bearing a smaller pompom in proportion, some plates adjoining the superomarginals having as few as 6 spinelets in the cluster; one or two small secondary abactinal plates occur around some of the proximal papular pores; there are 10 longitudinal rows of pores on each ray., the outermost of only 4 pores. The superomarginal plates are mostly smaller than the adjoining abactinal plates and are rounded or D-shaped; each bears a small pompom, the more interradial ones with up to *c*.15 spinelets. The inferomarginal plates project well beyond the superomarginals to form the edge of the body, their adradial parts are flattened dorso-ventrally but the free part is prolonged and constricted so as to be rounded in cross section and separated from the adjacent inferomarginals; each bears a laterally compressed cluster of numerous fine spinelets, the apical ones slightly coarser than the abactinal spinelets. The actinal plates are in regular

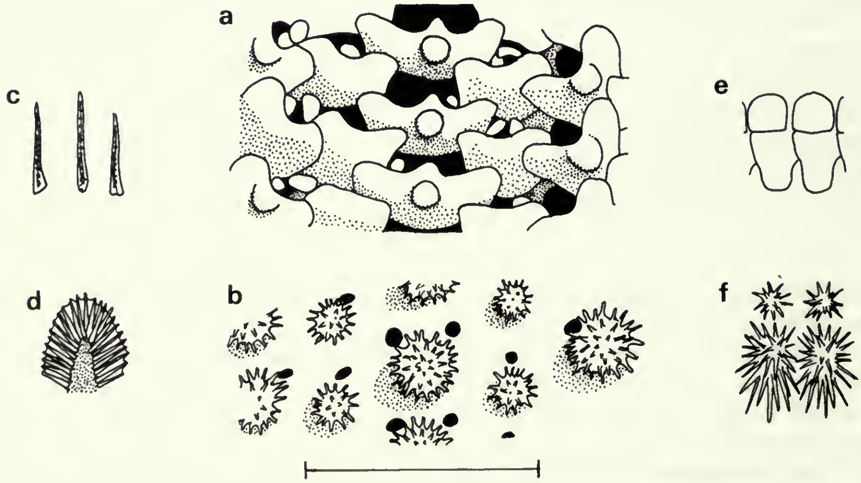

Fig. 8 *Paxillasterina pompom* gen. & sp. nov., holotype, USNM, Korbiski Reef, Atlantic side of Panama, R 14 mm (a) and (b) parts of denuded and intact proximal abactinal midradial areas; (c) three paxillar spinelets; (d) vertical section of one pompom (detached from column); (e) and (f) two pairs of marginal plates in dorsal view, denuded and intact (proximal to the left). The scale measures 1 mm for (c) and 2 mm for the rest.

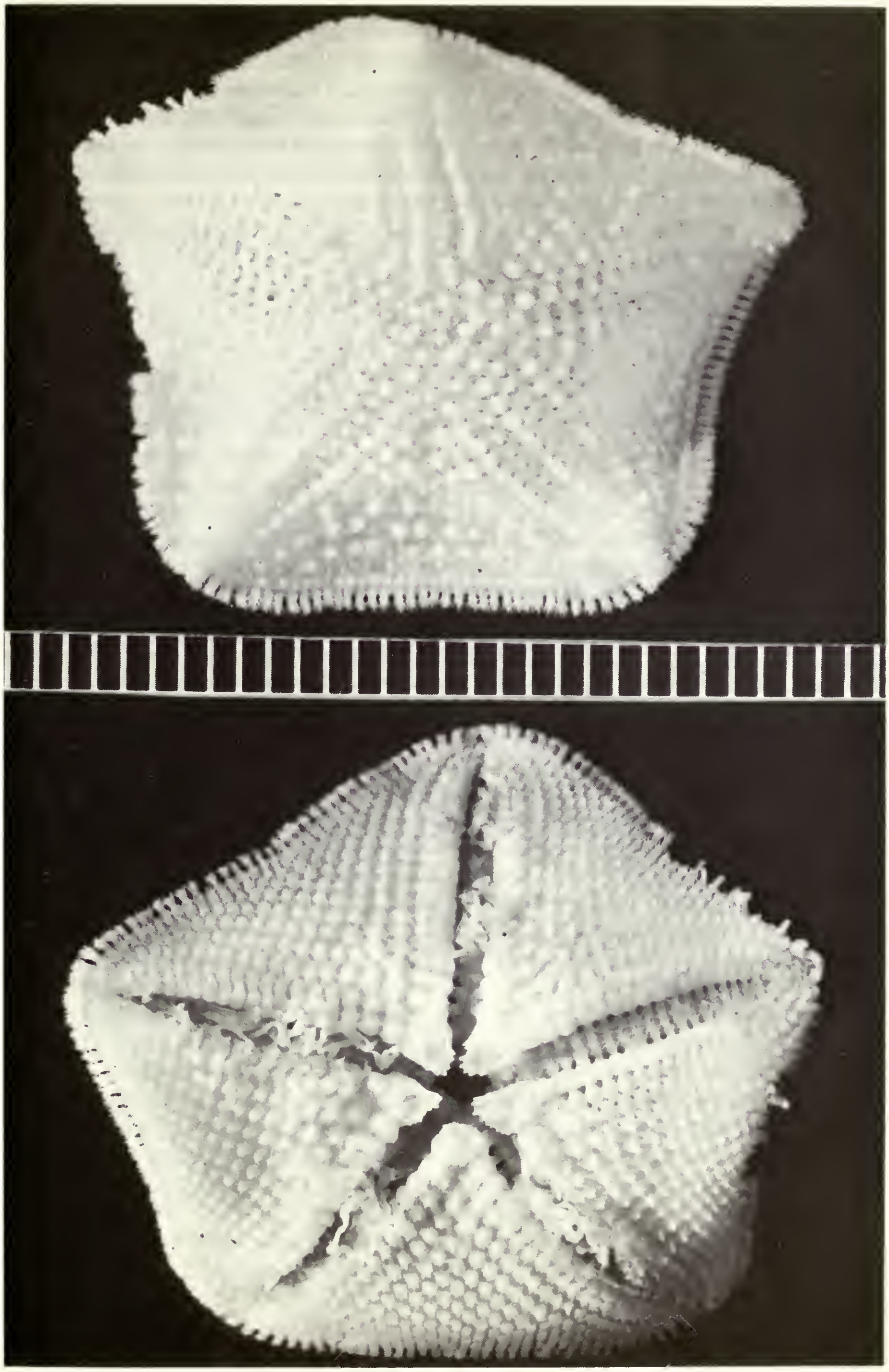

Fig. 9 *Paxillasterina pompom,* holotype, from above and below, ×4.

chevrons and each has two or three adradial lobes (distinct when denuded); each bears a tangentially-aligned fan of up to 5 spinelets, mostly 3 but the admarginal ones with 5, joined by skin. The adambulacral plates each have a shallow abradial step bearing a fan of subambulacral spinelets aligned slightly obliquely to the furrow and close behind the fan of furrow spines, which are slightly longer but arise at a higher level so that the tips project to about the same extent; each fan is usually of 4 spines or spinelets and webbed. Each jaw is armed with a larger fan of up to 16 spines, 7 or 8 on each oral plate, the apical ones about twice as large as the outermost; there is also a pair (or trio) of small suboral spinelets on each plate. The gonopores cannot be distinguished.

PARATYPES: Three other specimens are also available from the Atlantic side of Panama. One is also from Korbiski Reef but in 3 metres depth; it has R/r 15/11·5 mm and is similar to the holotype but for having usually 5 furrow spines. Another, from Mackerel Reef, also San Blas Is, was only collected two years ago and still shows traces of yellow colouration in spirit. The third is from 'Landing Craft Reef', south of the Galeta Marine Laboratory, Canal Zone, 'under rock in the coralline zone or higher'; it is dried and distorted with the pompoms mostly appressed horizontally; R is *c*.10 mm and the subambulacral spinelets usually number only 3.

Family **GANERIIDAE** Sladen

Asterinidae: Ganeriinae Sladen, 1889 : 375–376.
Ganeriidae: Perrier, 1894 : 171; Fisher, 1911*a* : 251 (in key); Verrill, 1914*b* : 365–366; Fisher, 1940 : 127; A. M. Clark, 1962 : 23–24; Bernasconi, 1964 : 59–60; Spencer & Wright, 1966 : U69; Blake, 1981 : 380–381 (pt). [Non Ganeriidae: A. H. Clark, 1938, Downey, 1973 (*Leilaster*)]
Asterinidae (pt): Madsen, 1956 : 22–23; Bernasconi, 1973 : 335–336 (*Patiria obesa*).
Goniasteridae (pt): Bernasconi, 1965 : 333–335 (*Vemaster*).

A family of Valvatida with body stellate, rarely almost pentagonal, interradial arcs rounded, arms normally five, rounded in cross-section except in the aberrant abyssal *Vemaster*; abactinal plates imbricating, usually paxilliform but the columns sometimes broadened and not well-defined, or coarse and tabulate, or with the basal lobes reduced and the plates obscured by thickened pustular body wall (in wet specimens of *Perknaster*), crowned with clusters of spinelets, which may be short and superficially appearing granuliform in *Ganeria,* some specimens of *Cycethra* and in *Vemaster*; papulae in small groups in the meshes between the primary plates, more numerous adradially; marginal plates ranging from blocklike and conspicuous to indistinguishable from the adjacent plates, aligned laterally or towards the ventral side when smaller (as usually in *Perknaster*), reduced to one slightly projecting series (presumed inferomarginals) in *Vemaster,* armed with oval groups of spinelets or spines, or one or two vertical combs when coarser, as in *Ganeria*; actinal plates imbricating adradially, tending to form oblique transverse as well as longitudinal rows, especially the latter, each armed with a group of spinelets or one or two larger spines, except in *Vemaster* where armament is rare and the plates are irregular and possibly secondary and limited to the interradii; adambulacral plates small, matching the adradial row of actinal plates, armed with two (or sometimes one) furrow spines and several subambulacral spines, often forming pairs parallel (or oblique) to the furrow or all the spines forming one (or two) series transverse to the furrow; pedicellariae absent (rarely a few spinelets forming a simple fascicle); internally a proximal interradial calcified pillar supporting the abactinal body wall dorsolaterally, no superambulacral plates.

Family **ASTERINIDAE** Gray

Asterinidae Gray, 1840 : 228; Perrier, 1875 : 27–28[292]; Sladen, 1889 : 374–376; Fisher, 1911*a* : 253–254; Verrill, 1913 : 477–481; 1914*b* : 262–263; 364–365; Fisher, 1919 : 409; Madsen, 1956 : 22–23; Spencer & Wright, 1966 : U68; Bernasconi, 1973 : 335–336; A. M. Clark & Courtman-Stock, 1976 : 75; Blake, 1981 : 380–391 (pt).

A family of Valvatida with body form usually pentagonal to stellate but sometimes the rays narrow and more or less finger-like, usually numbering five but occasionally more, the surface completely flat below (unless the whole body is arched upwards when it is concave) but variously convex above, ranging from very low, the body leaf-like, to high with almost cylindrical rays but still with a distinct ventro-lateral angle supported internally by overlapping extensions of the lateralmost abactinal and actinal plates, the angle culminating in the relatively small inferomarginals, or sometimes blunted by similar prominence of both marginal series (in *Nepanthia* and *Callopatiria*); abactinal plates superficially flattened or convex, sometimes with a low ridge bearing the armament and in one case (*Paxillasterina* nov.) with a low circular paxillar column, the primary radial and interradial plates of the disc often distinguishable by their regular shape, the larger lobed more adradial plates of the papular areas appearing more or less crescentic, imbricating adradially (the more lateral plates) or proximally (the more midradial plates), often two magnitudes of plates, at least adradially, with much smaller secondary plates subdividing or restricting the papular spaces proximal to the primary plates, often with considerable regularity of arrangement of all the plates, though this tends to become obscured in large specimens; abactinal armament of multiple small spinelets, sometimes granules, on the middle or raised part of the plate, or armament lacking when the skin is more or less thickened; papulae usually single, sometimes in small clusters, absent near the margin; superomarginal plates small, often distinguishable from the adjacent abactinal plates only by their position above (sometimes alternating with) the inferomarginal plates which are seen in transverse sections of the ray to be wedge- or pear-shaped or peg-like, appearing as a reversed keystone wedged in among the overlapping inner ends of the adjacent lateralmost abactinal and actinal plates, but in external view appear oval or rectangular; the very flattened genera *Anseropoda* (and probably also *Stegnaster* and *Tremaster*) with less massive reinforcement for the very narrow angle, the entire body except for a narrow midradial band strengthened by overlapping struts projecting from the abactinal and corresponding actinal plates to form a latticework; actinal plates imbricating adradially, forming more or less regular transverse or oblique series from furrow to margin, also tending to form longitudinal rows parallel to the furrow but the abradial plates sometimes irregular, armed with one or several spinelets, when multiple arranged in fans or clusters: adambulacral plates relatively small, matching the innermost actinal rows and with armament usually of similar magnitude, furrow spines in a fan or comb; pedicellariae, if present, usually simple alveolar with two, occasionally three, slightly curved spiniform valves, sometimes (*Nepanthia*) fasciculate with more numerous valves; internally a proximal interradial pillar supporting the abactinal body wall; superambulacral-like plates developed more or less regularly in the narrow-rayed genera *Nepanthia* and *Callopatiria* but absent elsewhere.

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Synopsis

Leilaster A. H. Clark, 1938 (family Ganeriidae) and *Mirastrella* Fisher, 1940 (family Asterinidae) are abstracted from these families and provisionally referred to the order Spinulosida, family yet to be determined.

Vemaster Bernasconi, 1965, is referred from the Goniasteridae to the Ganeriidae but may warrant isolation in a suprageneric taxon when the whole family is reviewed.

Patiria obesa (H. L. Clark, 1910) is found not to be an asterinid but is synonymized with *Cycethra verrucosa* (Philippi, 1857), family Ganeriidae.

Patiria Gray, 1840, type species: *P. miniata* (Brandt, 1835) is synonymized with *Asterina* Nardo, 1834.

Patiria miniata (Brandt, 1835), *P. pectinifera* (Müller & Troschel, 1842), *P. chilensis* (Lütken, 1859) and *P. stellifera* (Möbius, 1859), are referred to *Asterina*.

Patiria granulosa (Perrier, 1875) is a synonym of *Asterina miniata* (Brandt, 1835).

Patiria granifera Gray, 1847 and *P. formosa* (Mortensen, 1933) are referred to *Callopatiria* Verrill, 1913, revived.

Patiria pulla and *P. rosea* Koehler & Vaney, 1906, are synonymized with *Allopatiria ocellifera* (Gray, 1847).

Paxillasterina gen. nov. for type sp. *P. pompom* sp. nov. from Atlantic Panama is described.

The following taxa are thought to be in need of reassessment:
Ganeriidae: *Aleutiaster* A. H. Clark, 1939
Hyalinothrix Fisher, 1911*b*
Knightaster H. E. S. Clark, 1972
Tarachaster Fisher, 1913.
Asterinidae: *Patiriella* Verrill, 1867
'Patiria' obtusa Gray, 1847
'Enoplopatiria' siderea Verrill, 1913

Appendix—The generic name *Asterina* and its type-species

The first use of the name *Asterina* was by Nardo (1834 : 716) for the two species *Asterias minuta* Linnaeus and *A. exigua* Lamarck, neither one designated as type species. In 1836 L. Agassiz adopted *Asterina* Nardo and cited only *Asterias minuta* Linnaeus. The first formal type designation now traced is the apparently provisional one of Fisher (1906 : 1087) stating 'Type (?) *Asterina gibbosa* (Pennant). *Asterina minuta* (Olivi) Nardo = *Asterias gibbosa'*, repeated without the query and abbreviated to *'Asterias minuta* Olivi = *Asterias gibbosa* Pennant' by Fisher in 1911*a*: 254, while Verrill (1913: 479) modified it to *'A. minuta* Nardo = *A. gibbosa* (Pennant)'. *Asterias minuta* Linnaeus dates from the Fauna Svecica (1761 : 512) and was described from Norwegian waters in terms mainly comparative with *Asterias rubens*. In the 12th and 13th (Gmelin) editions of the 'Systema naturae' (1767 and 1791) the concept of *A. minuta* was extended to include first the *Asterina*-like seastar from American waters shown in pl. 5, figs 14 and 15 of Seba (1758) and then *A. minuta*: O. F. Müller, 1776, again from Scandinavia, and *A. minuta*: Fabricius, 1780, from Greenland. In none of these localities does the common European starlet widely known as *Asterina gibbosa* occur and Verrill (1914*a*) notes of [*A*] *minuta* Linnaeus, 1761 'There is nothing in the few words of description to show that it is not the young of *A. rubens* or some similar species.' At first sight, this appears to render *Asterina* Nardo a synonym of *Asterias* Linnaeus.

However, it is evident that Fisher was aware of this anomaly, hence his introduction of *'Asterias minuta* Olivi' (1792), a record from the Adriatic where *gibbosa* is found (also the recently recognized *Asterina phylactica* Emson & Crump but that diminutive species may be ignored in this context). Articles 69 and 70 of the Code of Nomenclature, on subsequent designation of type-species and deliberate use of misidentification, are intended to allow for this sort of problem so that the species which Fisher had in mind—namely *Asterias gibbosa* Pennant, 1777—is usable as type-species of *Asterina* Nardo. Evidence that this concept of *Asterina* is in accord with Nardo's lies in Forbes' use of *Asterina gibbosa* already in 1839.

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Peniculus haemuloni, a new species of copepod (Siphonostomatoida: Pennellidae) parasitic on *Haemulon steindachneri* from Ubatuba, Brazil

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Introduction

The genus *Peniculus* was established by Nordmann, 1832, to accommodate *Peniculus fistula,* a parasite of the teleost fish—*Diplodus annularis* Linnaeus (as *Sargus annularis*). To date 17 nominal species exist although according to Kabata (1979) at least two of them should be regarded as *species inquirendae*: *P. calamus* Nordmann, 1864 and *P. fissipes* Wilson, 1917, the latter probably being a synonym of the type species. The new species is the first record of *Peniculus* from Brazilian waters and the first record of *Haemulon* as a host for *Peniculus.* The structure of the appendages within the Pennellidae is so uniform that they are of little taxonomic value for species recognition. The key to the species of *Peniculus* is based on gross body morphology.

Description of new species

Peniculus haemuloni n.sp.

Adult female: The cephalothorax is about one tenth as long as the trunk (Fig. 1A), ovoidal, and flattened dorsally but convex ventrally (Fig. 1B) with a pair of rounded swellings anteriorly bearing the second antennae (Fig. 1D). The prominent mouth tube is directed posteroventrally (Fig. 1C). The four thoracic segments form a relatively short, uniformly slender neck comprising about one sixth of the trunk length. The neck is slightly flattened dorsoventrally and has a conspicuous internal system of longitudinal and transverse chitinous thickenings (Fig. 1C). Posteriorly the neck bears three pairs of swimming legs. The elongate subcylindrical trunk is slightly dorsoventrally flattened and comprises four-fifths of the total body length (Fig. 1A). A pair of terminal ventrolateral swellings bears the oviduct openings. The egg sacs are straight and uniseriate (Fig. 2B). The small rounded, dorsally placed abdomen bears two groups of four short setae (Fig. 2C) which are presumed to represent the caudal rami. The first antennae are absent. The second antennae are stout with a strongly curved terminal claw. The mouth tube is well developed extending almost to the posterior margin of the cephalothorax. The apex of the mouth tube has a circular opening surrounded by a thin membrane. The swimming legs comprise an oval flattened protopod and a 2-segmented exopod. The first segment is devoid of armature elements, the second has five setae on both the first and the third legs, the second leg armature was missing. Each limb pair is connected by a sternal bar (Fig. 2A). Dimensions of the holotype female: total length (exc. egg sacs) 5·6 mm; trunk length 4·4 mm; trunk width, 0·6 mm; neck length, 0·7 mm; neck width, 0·1 mm; cephalothorax length, 0·5 mm; cephalothorax width, 0·35 mm; egg sac width, 0·16 mm.

MATERIAL EXAMINED. Two adult females from the tail fin of the teleost *Haemulon steindachneri* collected at Ubatuba, Brazil (23°27′S: 45°06′W) by Dr K. Rohde in March 1979. The

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*Work completed during a six month secondment from the Department of Applied Biology, U.W.I.S.T. King Edward VII Avenue, Cardiff.

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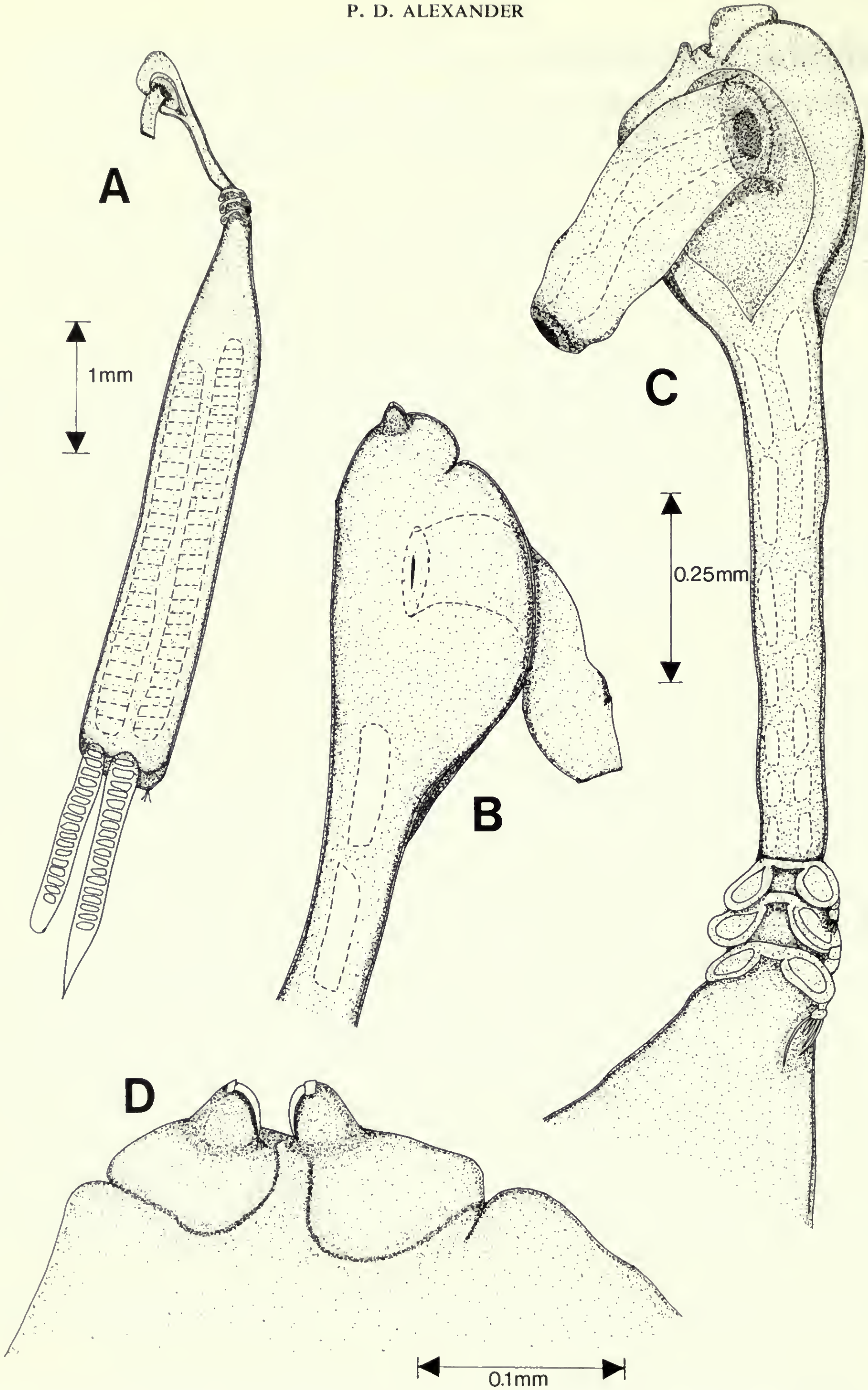

Fig. 1 *Peniculus haemuloni* n.sp. A, Female, ventral; B, cephalothorax, lateral; C, cephalothorax and neck showing mouth tube and internal chitinous framework, ventral; D, Anterior of cephalothorax showing second antennae.

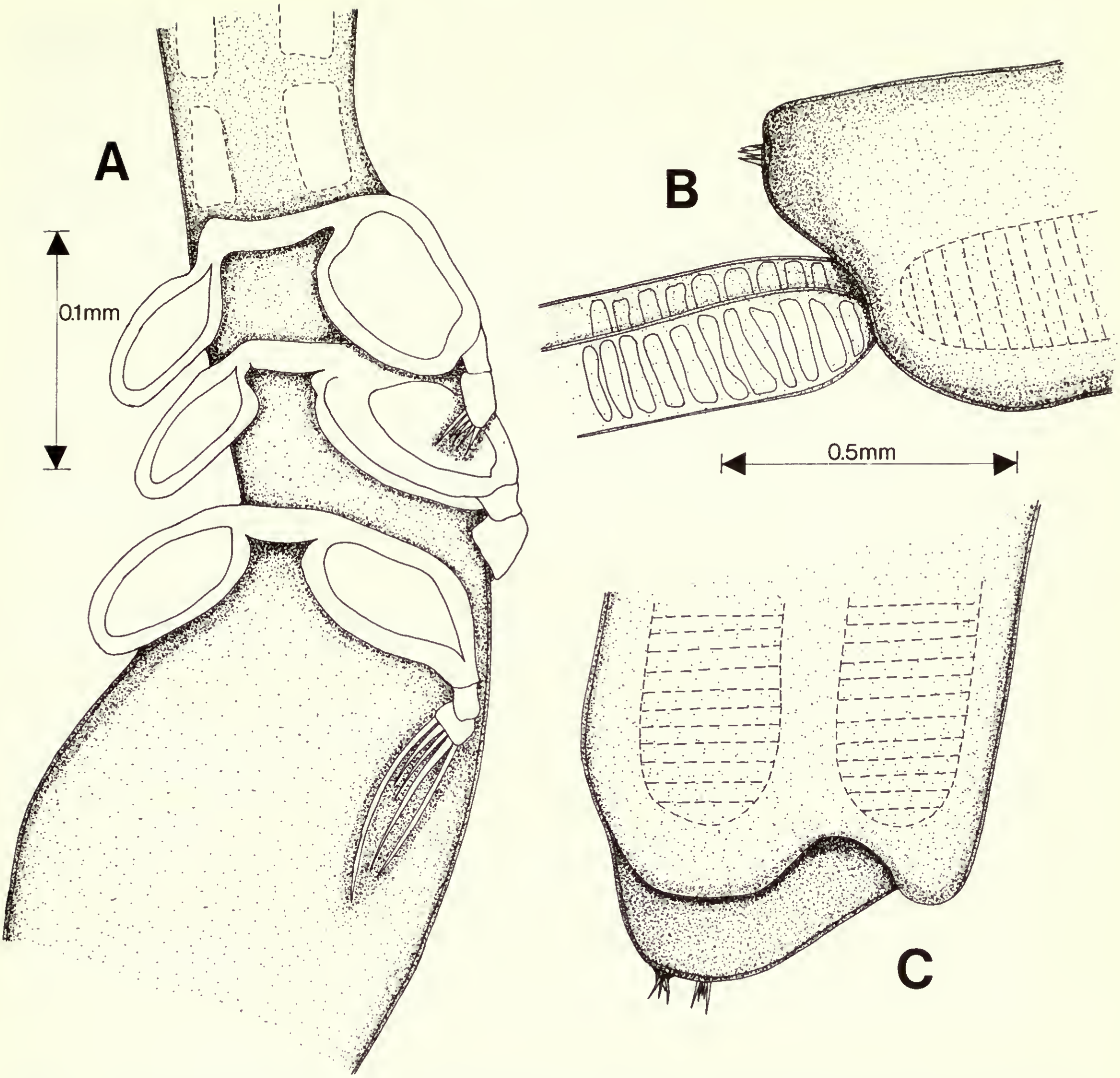

Fig. 2 *Peniculus haemuloni* n.sp. A, Structure and position of the three pairs of limbs, ventral; B, posterior region of trunk and egg sacs, lateral; C, posterior region of trunk showing caudal setae, ventrolateral.

ovigerous female is the holotype, registration number 1979.683; paratype female, registration number 1979.684. Both are deposited in the collections of the British Museum (Natural History), London.

REMARKS. The presence of only three pairs of swimming legs distinguishes *Peniculus haemuloni* n.sp. from most known species of the genus. Two other species, *Peniculus* sp. Kazatchenko & Avdeev, (1977) and *P. sciaenae* Gnanamuthu (1951*a*), have been described with three pairs of swimming legs. The former has the first two close together with a marked gap before the last pair at the base of the neck, whereas in *P. haemuloni* all three legs are close together at the base of the neck. It is probable that leg 1 of *P. sciaenae* was overlooked by Gnanamuthu (1951*a*) because this species appears to be closely related to *P. trichiuri, P. stromatei, P. theraponi* and *P. scomberi* although the last species apparently lacks legs in the adult female. All of these species were described by Gnanamuthu (1951*a, b*) each coming from a host belonging to a different family of teleost fish found in Indian waters. All possess a posterior swelling on the ventral surface of the cephalothorax and exhibit the same distribution of swimming legs, where present, along the neck and trunk. The differences between these species are relatively minor and it is possible that they represent forms of a single variable species.

Another useful character distinguishing *P. haemuloni* is the large prominent mouth tube which is similarly well developed in only two other species, *P. clavatus* Krøyer, 1863 and *P. fistula* Nordmann, 1832. The length to width ratio of the trunk (6·7 : 1) is most closely matched by that of *P. scomberi* (6·5 : 1) and *P. fistula* (6·3 : 1). These characters apart the new species shares many features with other *Peniculus* species, such as cephalothorax shape, the small rounded abdomen and the presence of a chitinous framework in the neck.

Key to the species of *Peniculus* (adult females only)

1	Cephalothorax with 4 large holdfast processes	***P. asinus*** Kabata
–	Cephalothorax without such processes	2
2	Cephalothorax with rounded swelling on ventral surface posterior to mouth tube	3
–	Cephalothorax without posterior swelling on ventral surface	6
3	Swimming legs apparently absent	***P. scomberi*** Gnanamuthu
–	Swimming legs present	4
4	3 pairs of swimming legs present	***P. sciaenae*** Gnanamuthu
–	4 pairs of swimming legs present	5
5	Trunk about 11 times longer than wide	***P. trichiuri*** Gnanamuthu
–	Trunk about 8 times longer than wide	***P. stromatei*** Gnanamuthu/***P. theraponi*** Gnanamuthu*
6	3 pairs of swimming legs present	7
–	4 pairs of swimming legs present	8
7	All 3 pairs of legs positioned close together at the base of the neck	***P. haemuloni*** n.sp.
–	Last 2 pairs of legs separated by a gap	***Peniculus sp.*** Kazatchenko & Avdeev
8	Legs 3 and 4 closer together than legs 1 and 2	***P. communis*** Leigh-Sharpe
–	Legs 3 and 4 further apart than legs 1 and 2	9
9	Trunk more than 6 times longer than wide	***P. fistula*** Nordmann
–	Trunk between 3 and 4·5 times longer than wide	10
10	Mouth tube forming a massive posteriorly-directed proboscis	***P. clavatus*** Krøyer
–	Mouth tube not forming posteriorly-directed proboscis	11
11	Cephalothorax ovoid	12
–	Cephalothorax widest near posterior margin and tapering anteriorly	***P. elegans*** Leigh-Sharpe
12	Abdomen well developed; longer than wide	***P. minuticaudae*** Shiino
–	Abdomen minute; posterior margin of trunk more-or-less straight	13
13	Trunk 4·3 times longer than wide; neck less than half as long as cephalothorax	***P. ostraciontis*** Yamaguti
–	Trunk 3·3 times longer than wide; neck more than half as long as cephalothorax	***P. truncatus*** Shiino

* N.B. There appear to be no reliable characters separating these two species.

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An Atlas of Freshwater Testate Amoebae

C. G. Ogden & R. H. Hedley

1980, Hardcovers, 222pp, £17.50 (£18.00 by post). Co-published by British Museum (Natural History) and Oxford University Press.

This book illustrates, using scanning electron micrographs, most of the common species of testate amoebae that are found in freshwater habitats. Information on the biology, ecology, geographical distribution and a classification are followed by descriptions of ninety-five species. Each of these is illustrated by several views of the shell.
The text is designed not only to enable biologists to identify species of testate amoebae, but to serve as an introduction to students interested in the taxonomy and biology of these freshwater protozoa. It will be of special interest to protozoologists, ecologists, limnologists, water treatment specialists and micropalaeontologists interested in recent sediments.

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